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Full Name of Author — Nom complet de l'auteur
THOMAS BRUCE HERMAN

Date of Birth — Date de naissance
26 OCTOBER 1949

Country of Birth — Lieu de naissance
U.S.A.

Permanent Address — Résidence fixe
BIOLOGY DEPT
ACADIA UNIV.
WOLFVILLE, N.S. B0P 1X0

Title of Thesis — Titre de la thèse
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Name of Supervisor — Nom du directeur de thèse
F.-S. CHIA

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THE UNIVERSITY OF ALBERTA

POPULATION ECOLOGY OF INSULAR
Peromyscus maniculatus

by

Ⓒ THOMAS BRUCE HERMAN

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
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FALL, 1979

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "Population Ecology of Insular *Peromyscus maniculatus*" submitted by Thomas Bruce Herman in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

....
Supervisor

Curtis Strobeck
....

....

....

Mark V. H. Wilson
....

Charles J. Krebs
....
External Examiner

Date 7 September 1979

ABSTRACT

Populations of the deermouse *Peromyscus maniculatus* were studied by capture-mark-recapture trapping and dead-trapping on the mainland of Vancouver Island and on 24 small (5-1685 ha) forested islands in adjacent Barkley Sound between January 1976 and October 1977.

Island and mainland population densities did not differ consistently. Densities varied among islands, but showed no relationship with island size. Variance of population size through time was lower on some islands than on the mainland.

Reproductive activity was generally synchronous on islands and mainland in 1977, but in 1976 breeding in island populations extended into winter. Litters were smaller on islands than on the mainland, but litter size did not vary significantly among islands.

Juvenile recruitment in mainland populations occurred mainly at the end of the breeding season, but in some island populations was dispersed throughout the breeding season.

Behavioural interactions of breeding males from three islands and the mainland were observed in an arena. Among islands mice were most aggressive on the smallest (13 ha) and most cohesive and least aggressive on the largest

(175 ha). The latter did not differ from mainland mice in cohesiveness or aggressiveness.

Tail wounding was more common in island males than in mainland males, and among islands wounding levels appeared to increase with decreasing island size.

Pre-natal mortality was low at all locations and did not differ consistently between island and mainland populations. Pre-weaning mortality was apparently high at all locations, especially on islands in 1976, where, despite prolonged and intensive breeding, recruitment of young was low. Survival of juvenile recruits (particularly males) to sub-adulthood was lower on some but not all islands than on the mainland. Age distributions of males were top-heavy on most but not all islands; this tendency generally increased with decreasing island size. Age distributions of females varied little among islands, or between islands and mainland. Sex ratios generally favoured males and did not differ significantly among island or between island and mainland populations.

Prevalence of the parasitic nematode *Capillaria hepatica*, used in past studies as an indirect indicator of cannibalism, was higher in island than in mainland populations. Among islands prevalence and severity of infections were inversely proportional to island size. Wounding indices and *C. hepatica* prevalences from each island were in general positively correlated, but high

prevalence on islands may only indicate increased intraspecific necrophagy by mice due to decreased abundance of competing scavengers.

Island mice were larger than mainland mice. Body weights varied among islands and in both sexes appeared to increase with decreasing island size. Body length/tail length ratios of island mice varied greatly among islands but consistently exceeded those of mainland mice.

Due to relative scarcity of predators on the islands, most mortality in island populations is likely directly or indirectly effected intraspecifically. Island deermice appear to avoid overpopulation by eating surplus animals, rather than by reducing reproductive effort.

To explain the extensive variation in life history parameters encountered among islands requires more detailed knowledge of the deermouse's environment.

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INTRODUCTION

Islands have fascinated naturalists and biologists for many years. The contributions that early insular studies made to the development of evolutionary and biogeographic theory were profound (Darwin, 1859; Wallace, 1869, 1880). Islands are appealing for several reasons. As natural, self-contained laboratories, they represent "microcosms of evolution and population biology" (Carlquist, 1971). With recognition of the essentially insular nature of many continental environments, we realize the wide applicability of lessons learned on islands.

Insular faunas and floras tend to be structurally simple and depauperate of species in comparison to their continental counterparts. Although long recognized, this widespread phenomenon has received increased attention since the publication of MacArthur and Wilson's (1967) equilibrium theory of island biogeography. This work has prompted numerous studies of distribution on islands, and of the roles played by colonization and extinction (for a review, see Simberloff, 1974).

Despite the diversity of form that insular organisms exhibit, many groups appear to share common structural and functional properties. Morphological traits such as gigantism and dwarfism, and aspects of reproductive biology have received wide interest (Carlquist, 1965, 1974). These phenomena prompted MacArthur and Wilson (1967) to ask how natural selection acts on islands and how it may act differently on islands than on mainlands.

If there are patterns in insular distributions and ecological strategies, what mechanisms are responsible and how do we predict the distributions and strategies?

We generally accept the search for patterns as a central activity of science, but we frequently forget that it is necessary to set limits when constructing generalities. MacArthur (1972) emphasized this when looking for biogeographic patterns, and was careful to point out that groups of organisms should share the same morphology, economics, and population dynamics, and should be found in environments of the same structure before they can be expected to exhibit a pattern.

Detailed studies of these attributes and their interactions in insular populations are uncommon, but they are necessary before we can understand the processes of natality, mortality, and migration, which ultimately determine the abundance and distribution of any organism. What insular organisms might be appropriate for such studies?

As a group, small mammals occur frequently on near-shore islands. Because of their relatively poor dispersal abilities, adjacent populations may remain isolated despite their proximity to one another. Once isolated, some members of this group exhibit rapid evolution (Corbet, 1961; Berry, 1964; Foster, 1965).

There are numerous islands on the coast of British Columbia. Many support populations of the deermouse, *Peromyscus maniculatus*, which is common in woodland and grassland habitats on the adjacent mainland and throughout much of North America. Although well known for its phenotypic plasticity (Kavanau, 1967) this species exhibits similar patterns of annual abundance and reproductive behaviour over wide geographic areas (Terman, 1968; Fairbairn, 1977) and, despite its immense range, is relatively uniform in genic composition, in comparison to other species groups in the genus (Avise et al., 1979). Until recently, studies of insular British Columbia *Peromyscus* dealt chiefly with taxonomic questions (McCabe and Cowan, 1945; Foster, 1965). Although apparent demographic and morphological patterns emerged from these studies, detailed information on the dynamics of individual populations was lacking. In an attempt to fill this gap, Redfield (1976) collected information on the distribution, abundance, and size of deermice in the Gulf Islands between the mainland and southern Vancouver Island, and related these data to current biogeographical theory. More recent studies of dispersal (Sullivan, 1977) and behaviour (Halpin and Sullivan, 1978) in the same area have helped to elucidate ecological strategies of insular deermice.

Unfortunately, natural and man-induced heterogeneity of habitat structure complicates comparison among the Gulf Islands, and differences in environmental severity complicate comparisons with the adjacent mainland. In the Barkley Sound region on the west coast of Vancouver Island these problems can largely be avoided. Barkley Sound contains numerous islands that range in size from less than 1 to more than 1700 ha. They are relatively homogeneous, comparable in habitat structure, and undisturbed by human activity. In addition, large tracts of similar undisturbed lowland forest are available on the adjacent mainland (of Vancouver Island) for comparative purposes.

The geologic history of these islands is similar to that of the Gulf Islands. Both groups have been isolated in their present configurations for at least 5500 years (Mathews et al., 1970; Carter, 1971), but were previously joined to the mainland. This evidence, combined with the pattern of distribution, and the lack of evidence of either genetic exchange between islands or contemporary colonization led Redfield (1976) to conclude that *Peromyscus* is a poor disperser to nearshore islands and that Gulf Island populations are not in dynamic equilibrium, but are in a sense relicts. Foster (1965) drew the same conclusion for deermice in the Queen Charlotte Islands. Crowell (1973) concluded that deermice off the coast of Maine are relatively poor dispersers but good persisters.

The same is likely true for deermice in the Barkley Sound area, where a qualitative inventory of insular mammals (Guiget, 1974) revealed no *Peromyscus* on islands of less than 5 ha (n = 19), regardless of their proximity to the mainland or inhabited islands. No islands greater than 22.5 ha (n = 21) lacked deermice, and in the intervening size range, 15 islands contained mice and 13 did not. One might infer from this that islands larger than 22.5 ha support persistent populations, while islands smaller than that size may not.

If persistent insular populations of *Peromyscus* exist, what ecological strategies promote persistence? How much variation in strategy is there among islands and what are the effects of island size? How do these strategies differ from ecological strategies in mainland populations?

Since vertebrate populations on nearshore islands formed by rising eustatic sea level are less likely to experience founder effect (Mayr, 1954) than those on oceanic islands, it is more likely that variations observed among nearshore populations are due to natural selection than to random and unpredictable events (Soulé, 1966). Therefore, if these populations do exhibit underlying patterns, accommodation of the exceptions, which directs us toward the ultimate explanation of any pattern, should be easier.

Islands are paradigms for geographic entities of all sizes, and one might expect gradual changes in strategy along an island size continuum which ranges from very small to continental. This may be unrealistic; while some dimensions of an animal's environment change gradually with island size, other dimensions, such as the presence/absence of a competitor or predator, change abruptly. Therefore, populations may show gradual or no changes within specified island size classes and abrupt changes between those classes.

Regardless of the pattern of change, processes affecting a population's ability to persist likely vary with the size and degree of isolation of the population. MacArthur (1972) considers extinction to be the result of four potentially interacting factors: predation (including disease), competition, habitat alteration, and random population fluctuations. In large populations the probability of extinction from random population fluctuations is low, but in small populations it is high.

On small islands, species frequently lack predators and interspecific competitors, and the role of random fluctuations becomes increasingly important in extinction processes.

The probability of random extinction is not only a function of population size, but also of the variance of that size. Therefore in populations that have persisted on small islands, selection may have favoured attributes that maintain relatively high numbers and dampen population oscillations. Crowell (1973) suggested that an insular species should minimize turnover and r (instantaneous rate of increase) by reducing the birth rate as the population approaches K (carrying capacity), and he observed a phenotypic "K-response" in introduced island populations of *Peromyscus maniculatus* off the coast of Maine.

MacArthur and Wilson (1967) present a model by which r-selection and K-selection may be in opposition, and stress that persistent island populations occupying relatively stable habitats should undergo strong K-selection in comparison to their mainland counterparts.

Although the usefulness of "simplistic" theoretical models in the explanation of ecological strategies may be limited (Wilbur et al., 1974; Southwood et al., 1974; Nichols et al., 1976; Stearns, 1976), these models help us to approach organisms as systems of co-adapted traits and encourage us to consider interactions among those traits (Stearns, 1976). If we assume that climatic regimes are milder and vertebrate predation pressures are less severe on temperate nearshore islands than on temperate mainlands, a summary of some of the correlates of r- and K-selection (Table 1) suggests that this model may provide an appropriate framework from which we can generate predictions of ecological strategies in insular and mainland populations of *Peromyscus*.

Increased densities in insular populations are commonly reported, but the causal mechanisms invoked are quite varied. Crowell (1962) attributed increased densities of individual bird species on Bermuda to decreased interspecific competition. Soulé (1966) found increased densities in insular iguanid lizard species and suggested that if food is either directly or indirectly limiting, these increases may occur because the gene flow which inhibits adaptive ecological shifts on the mainland is missing on small islands. Krebs et al. (1969) demonstrated that fenced vole populations increased in density because they were unable to emigrate. MacArthur (1972) suggested that the "Krebs effect" could be important on small islands and that it must eventually disappear as island size increases, but was unable to detect its presence in bird populations in the Pearl Archipelago. Lidicker (1975) proposed that small islands may lack dispersal sinks and subsequently experience "frustrated" dispersal; and he provided a model by which selection in evolutionary time would reduce the perceived level of frustrated dispersal and allow population density to increase to carrying capacity. Mazurkiewicz (1972) noted increased densities of *Clethrionomys glareolus* on a small island in Poland and concluded that lack of dispersal was responsible. Redfield (1976) suggested that increased densities of *Peromyscus maniculatus* in the Gulf Islands could be due to either the "Krebs effect" or to some kind of "group selection" for high density to avoid extinction, although he did not offer any specific mechanisms for the latter. Tamarin (1977a,b) concluded that the consistently high densities of the insular vole *Microtus breweri* were largely responsible for the development of a "K-strategy" in that species.

There are few reports of dampened density oscillations in insular small mammals. Tamarin (1977b) observed them in *Microtus breweri*, and Redfield (1976) and Sullivan (pers. comm.) suggested that they may occur in Gulf Island *Peromyscus* populations, but most studies have been too short in duration to measure them. A decrease in individual litter size with an increase in the length of the breeding season might help dampen oscillations, and there is some evidence for this in Gulf Island *Peromyscus* populations

(Sullivan, 1977). Decreased reproductive effort in general, which is also a correlate of K-selection and which should dampen oscillations, is widely reported in vertebrate populations from small islands (Carlquist, 1974; Clough, 1969; Kramer, 1946; Lack, 1971; Tamarin, 1977a,b).

Density oscillations may also be affected by recruitment patterns. Deermouse populations in coastal coniferous forest of mainland British Columbia exhibit a bi-modal pattern of juvenile recruitment with a major peak at the end of the breeding season (Sadleir, 1965; Petticrew and Sadleir, 1974; Fairbairn, 1977). Sadleir (1965) and Healey (1967) attributed this pattern largely to agonistic behaviour by reproductively active adult males toward juveniles, and suggested that it plays a key role in population regulation. However, in Gulf Island populations juvenile recruitment is evenly dispersed throughout the breeding season (Sullivan, 1977). This may act to dampen density oscillations, but it also raises the question of what role agonistic behaviour may play in insular populations.

Several studies suggest a causal link between agonistic behaviour and dispersal in mainland British Columbia *Peromyscus* (Sadleir, 1965; Healey, 1967; Fairbairn, 1976, 1978). However, on small islands selection should minimize dispersal tendencies (Van Valen, 1971). There is good evidence for this in Gulf Island *Peromyscus* (Sullivan, 1977) and in *Clethrionomys glareolus* from Poland (Mazurkiewicz and Rajska, 1975). In addition, Halpin and Sullivan (1978) have shown that Gulf Island deermice tend to be less aggressive and more cohesive than their mainland counterparts. They suggest that reduced competition for food (due to high food levels and/or absence of interspecific competitors) and the frustration of dispersal may be the most important factors reducing agonistic behaviours in the island populations. A lack of aggressiveness also occurs in other insular small mammal populations (Clough, 1969; Tamarin, 1977a).

Avoidance of risk is obviously advantageous in small isolated populations. High risk reproductive strategies such as early breeding during times of low energy availability, observed by Fairbairn (1977) in mainland west coast deermice, should be absent on small islands because of the high variance in reproductive success associated with these strategies (Roff, 1974). The duration of the breeding season in coastal *Peromyscus* is largely controlled by energy availability (Sadleir et al., 1973), and all other things being equal, one might predict shorter breeding seasons in insular populations. Jewell (1966) observed this in several small mammal species on small islands in Great Britain. However, energy availability on islands may be affected by climate, and by levels of interspecific competition and predation (Grant, 1965; Van Valen, 1973; Case, 1978; Heaney, 1978). Island populations tend to experience milder climatic regimes than their mainland counterparts and reduced levels of interspecific competition. Although Gulf Island deermice do not show a separate early breeding peak, they do tend to breed for a greater part of the year than mainland populations (Sullivan, 1977). If juvenile recruitment is evenly dispersed throughout the breeding season, an increase in the length of that season might further dampen oscillations in density.

Decreased predation on islands may strongly affect the evolution of ecological strategies (Grant, 1965; MacArthur and Wilson, 1967; Case, 1978; Heaney, 1978). Direct short term effects may include changes in mortality or survivorship patterns, with an eventual evolutionary increase in longevity. Increased longevity is common in insular organisms (Carlquist, 1974). Foster (1965) found older age distributions in deermouse populations from the Queen Charlotte Islands than from the adjacent mainland. Redfield (1976) reported a top-heavy age distribution in Gulf Island deermouse populations, and suggested that individuals may live longer and reproduce at lower intensities than those on the mainland. Kramer (1946) and Tamarin (1977c,d) both invoked lack of predation as a causal factor in the evolution of the strongly "K-selected" characteristics displayed by their insular lizard and vole populations respectively.

Charnov and Schaffer (1973) emphasized the importance of separating juvenile and adult mortality, but it is often difficult to measure accurately mortality in small mammal populations. Krebs et al. (1969) and Bujalska (1975) showed that mortality of juveniles is important in enclosed and insular vole populations, while in open and mainland populations mortality of adults and subadults is probably of greater importance.

In the absence of interspecific predation, intraspecific mortality factors may become important in insular populations. Tamarin (1977a) observed higher pre- and post-implantation mortality in insular voles than in those on the mainland. Kramer (1946) found that cannibalism was common in island populations of the wall lizard (*Lacerta sicula*) but rare in adjacent mainland populations. Cannibalism has also been reported in enclosed small mammal populations (Southwick, 1955; Boice, 1972). Ullyett (1950) showed that cannibalism increases stability and persistence of blowfly populations in the lab; and Fox (1975) presented a convincing argument for the potential role of cannibalism as a population regulator. Unfortunately, it is nearly impossible to measure cannibalism in natural populations of small mammals, although Freeman and Wright (1960) used infection levels of a parasitic nematode, *Capillaria hepatica*, as an indirect indicator in Ontario populations of *Peromyscus maniculatus*.

Several morphological traits that commonly occur in insular vertebrates have been attributed to relaxed predation pressure. Shorter appendages and tails occur in some insular lizard populations that lack predators (Kramer, 1951), and Foster (1965) showed a clear correlation between body/tail length ratios and presence/absence of quadrupedal predators in island populations of *Peromyscus maniculatus*. Increased body size frequently occurs in insular rodent populations that lack ground predators (Cook, 1961; Coutts and Rowlands, 1969; Carlquist, 1974); and Delany (1970) showed that individual *Apodemus sylvaticus* are smaller on islands that contain ground predators than on those that do not. Corbet (1961) suggested that intraspecific selection would favour large size, and therefore size could increase rapidly in island forms due to the absence of ground predators. Fifty years after an inadvertent experimental introduction of *Rattus rattus* to a small island containing deermice in the Queen Charlotte Islands, the deermouse population showed significant decreases in mean body size and mean body/tail ratio from measurements taken before the introduction (Foster, 1965). Recently, Heaney (1978) and Case (1978) have taken a comprehensive multi-factor approach to explaining insular body size trends in mammals (Heaney) and in terrestrial vertebrates in general (Case).

An increase in body size may in itself lead to an increase in longevity because of the inverse relationships between metabolic activity and body weight and between metabolic activity and life span (Bourlière, 1957). From this Southwood et al. (1974) predicted that larger organisms would be less susceptible to short term climate change and therefore would perceive their environments as more stable. However, intraspecific size differences may be too small to show this effect.

The above account has led me to ask the following questions: Do mainland and island populations of *Peromyscus maniculatus* from the Barkley Sound region differ? Do ecological strategies differ among island populations, and if so, what are the effects of island size? If differences exist, are they compatible with theoretical predictions made by island biologists to date? Is it possible to separate environmental and evolutionary components in these differences?

With these questions in mind and in view of the existing knowledge of insular *Peromyscus*, the following hypotheses can be established. For origins of and detailed rationale behind these hypotheses, see sources in parentheses. This study is an attempt to test these hypotheses:

1. Density increases with decreasing island size (Krebs et al., 1969); MacArthur, 1972; Lidicker, 1975).

2. Island populations exhibit lower amplitude density oscillations through time than adjacent mainland populations (MacArthur, 1972).

3. Onset of seasonal reproductive activity is increasingly delayed with decreasing island size (Roff, 1974; Fairbairn, 1977).

4. Litter size is lower in island populations than in mainland populations, and decreases with decreasing island size (MacArthur and Wilson, 1967).

5. Juvenile recruitment is more evenly dispersed through the breeding season on islands than on the mainland (Sullivan, 1977; Halpin and Sullivan, 1978).

6. Agonistic behaviour of sexually active resident adult males toward each other diminishes with decreasing island size (Tamarin, 1977a; Halpin and Sullivan, 1978).

7. Intraspecific mortality factors play a relatively more important role in island populations than in their mainland counterparts. Insular populations show:

a) higher in utero mortality (Tamarin, 1977a)

b) older age structure (Carlquist, 1974; Redfield, 1976)

c) higher frequency of cannibalism (Kramer, 1946; Southwick, 1955; Fox, 1975).

8. In addition, in the absence of quadrupedal predation insular populations should show the following morphological attributes relative to their mainland counterparts:

a) increased body size (Corbet, 1961; MacArthur and Wilson, 1967)

b) increased body/tail length ratios (Kramer, 1951; Foster, 1965).

MATERIALS AND METHODS

Study Area

Barkley Sound lies on the west coast of Vancouver Island (48°50'N., 125°15'W.) (Figure 1). All populations sampled in this study were from islands in the Sound or from the mainland (of Vancouver Island) immediately adjacent to the southeastern quarter of the Sound. The entire study area falls within the "Northern Pacific Coast" section of the "Coast Forest Region" (Rowe, 1972), the principal associates of which include western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), amabilis fir (*Abies amabilis*), and sitka spruce (*Picea sitchensis*).

The topography of the area is rugged and mountainous; and soils are generally shallow, poorly developed, and acidic.

Precipitation is seasonal, with most occurring during the winter months, and is abundant, although annual variation can be substantial. In addition, due to the rugged topography, local variations may occur. Annual total precipitation in the village of Bamfield between 1973 and 1976 varied from 263 cm (1976) to 358 cm (1974), with an average of 310 cm (Janitis, pers. comm.).

Trapping Techniques and Schedules

Live-trap transects. In late 1975 pairs of permanent live-trapping transects were established on three islands of varying sizes in Barkley Sound (Haines, 13 ha; Helby, 71 ha; Diana, 174 ha) and at two locations on the adjacent mainland. Each transect was 150 m in length and consisted of 16 evenly spaced trap points. This trapping configuration has proven highly efficient and appropriate for work with *Peromyscus maniculatus* in coastal British Columbia (Petticrew and Sadleir, 1970). Members of each transect pair were well separated (minimum distance ≃ 150 m), and all transects were located a minimum of 75 m from prominent edges such as shorelines and roads.

Population monitoring on these transects commenced in February 1976 and continued at monthly intervals for 21 months. Each pair of transects was trapped simultaneously for two successive nights, during which four Longworth® traps containing sunflower seeds and terylene bedding were placed within a 3 m radius of each trap point.

All mice captured were individually marked by toe-clipping. At each capture the date, location along the transect, body weight to the nearest 0.5 g, pelage (juvenile, sub-adult, adult), and reproductive condition were recorded. Visible wounds and/or scars and infestations of ectoparasites were also noted. Males with large, fully or partially descended testes and females with perforate vagina, pregnancy plug, palpable embryos, or prominent mammae were considered to be reproductively active.

Vegetational similarity among locations was evaluated for three 'layers' (canopy, understory/shrub, herbaceous) with a technique revised from Canfield (1941). Dominance was measured along each live-trap transect by estimating the two most prevalent species (including the absence of all species) by percent cover in each 10 m segment of the 150 m transect for each layer.

In addition, a "deadfall index" was calculated along each transect. This was defined as the number of felled trunks and limbs exceeding 10 cm diameter (at the point of intersection with the transect) with at least one half of the cross-section above ground level.

Ross Islets introductions. In November 1976, a group of mice from Helby Island and a group from the mainland were introduced to two adjacent uninhabited and similar islets (approximately 1 ha) in Barkley Sound. Each group contained 16 individuals: four reproductively mature but inactive adults and four apparently reproductively immature adults of each sex. These populations were monitored with 11 quartets of Longworth® live-traps on each islet for two successive nights at monthly intervals from January 1977 to October 1977. This was done to test the hypotheses concerning differences in onset of breeding activity, and differences in the pattern of juvenile recruitment and mortality between island and mainland animals living in similar environments.

Dead-trap transects (monthly). Systematic dead-trapping was carried out with Museum Special® break-back traps baited with peanut butter. From February 1976 to January 1977, mouse populations from three islands (Fleming, Diana, and Helby) and from at least two mainland sites were sampled for two successive nights each month along transects containing 50 pairs of traps spaced at 10 m intervals. Transects were positioned differently from month to month at each site in order to avoid trapping areas from which mice has been previously removed. In order to estimate the numerical and spatial impact of "edge effect," all transects began close to the forest edge and were oriented perpendicularly to the shore on islands and perpendicularly to the shore or to roads on the mainland.

Dead-trap transects (blitz). In a six-week period from mid-May to late June 1977, mouse populations from 22 islands in Barkley Sound and from 10 locations on the adjacent mainland were sampled for one night along transects containing 25 quartets of Museum Special® break-back traps spaced at 10 m intervals. All populations on islands exceeding 15 ha were sampled with two transects simultaneously, and those on islands smaller than 15 ha were sampled with one transect. In order to minimize "edge effect" nearly all island transects were set a minimum of 100 m from shore and all mainland transects were set a minimum of 100 m from shore or roads.

Catch per unit effort was calculated for each dead-trap transect by dividing the number of mice captured by the number of trap nights. The number of trap nights was adjusted for traps sprung but empty according to Nelson and Clark (1973).

All mice collected by dead-trapping were weighed to the nearest 0.1 g. Standard measurements (total length, tail length, hindfoot length), pelage colouration (juvenile, sub-adult, adult), and external evidence of body wounding were recorded. Presence of tail wounding was noted and classified as light, moderate, or severe. In all females, condition of the vagina and development of the mammae were also recorded.

During necropsy of males, testis position and size (length x width), size of epididymis and presence or absence of visible tubules, and size of seminal vesicles were recorded.

During necropsy of females, thickness and vascularization of uterus were noted, and placental scars were counted and classified as old or new. Embryos present (including those partially resorbed) were counted, measured (crown-rump length), and weighed to the nearest 0.1 g. Ovaries were examined, and large follicles and/or corpora lutea were counted. Degree of development of mammary tissue was also noted.

In all necropsies stage of moult, presence and extent of body wounds and scars, and extent of subdermal and mesenteric fat deposits were recorded.

After February 1976 all skulls from necropsied animals were cleaned and saved for relative age determination by tooth wear, according to Foster (1965). In addition, livers were examined for parasitic infections and other abnormalities.

Arena Experiments

During the summer of 1977 behaviours of adult reproductive male deermice were observed in the laboratory. A total of 20 animals each from Haines, Helby, and Diana Islands and from two locations on the mainland was tested for social interactions. Mice were collected from the two live-trap transects at each location. In all cases only animals from the same location were tested together; ten random pairs, with one member from each transect (in order to avoid testing neighbours) were chosen and tested only once. At locations where ten reproductively active males were not obtained along each transect, samples were enhanced with mice collected from two additional areas at each location.

The test arena consisted of a large Plexiglas rectangular box divided into three compartments. The two end compartments (each 60 x 60 x 40 cm) were connected to a central compartment (60 x 40 x 40 cm) by means of four circular openings (each 5.0 cm in diameter) near the floor of the arena. These could be opened or closed from the outside by means of sliding Plexiglas panels. The top of the box was covered with hardware cloth to prevent escapes. The floor was covered with fresh cedar shavings, which were removed and replaced after each series of encounters.

Mice were introduced to the test arena during the first dark portion of the light cycle following removal from the field. Members of each pair were placed in opposite ends of the arena for a 5-minute habituation period before connections between compartments were opened. After the first entry of a mouse into the central compartment, all interactions between members of a pair were recorded for a 10-minute period. All observations took place under a 60 watt red light bulb.

Behaviours were classified according to Eisenberg (1968). All social behaviours were assigned to one of four major groups (after Halpin and Sullivan, 1978):

(1) approach - one animal turns toward and approaches the other animal, (2) investigatory - nasonasal and nasoanal sniffing, and sniffing of any other part of the body, (3) cohesive - huddling and allogrooming, and (4) agonistic. Agonistic behaviours included both aggressive behaviours (attack leap, side display, chasing, fighting, boxing, threat, rush, and bite) and defensive behaviours (avoidance, defensive uprights, submission, flight, and escape leap).

Mice were replaced at their points of capture at mainland locations immediately after completion of a test series, and at island locations in the morning following a test series.

Parasitic Infections

The presence of the parasitic nematode *Capillaria hepatica* was determined during necropsies of snap-trapped animals by gross examination of the liver for the characteristic ova and lesions (Freeman and Wright, 1960; Layne, 1968). Infections were classified as present (light and moderate) or heavy on the basis of extent and appearance on the liver surface (Layne, 1968; Luttermoser, 1938). Histological examination of a subsample of livers representative of the range of surface appearances confirmed the validity of this classification. Livers were also examined for the presence of encysted metacestodes or other abnormalities.

Livers were examined in 1272 mice from the monthly dead-trap transects, and in 451 mice from the blitz dead-trap transects.

In order to determine the usefulness of *C. hepatica* as an indirect indicator of cannibalism (= intraspecific predation) in these deermouse populations, an attempt was made to assess the relative importance of various modes of transmission of the worm in each population. Therefore the roles which predators and scavengers might play in the distribution of the parasite were examined.

In order to evaluate the potential role of scavengers in the distribution of *C. hepatica*, an attempt was made to measure relative abundance of shrews and of scavenging invertebrates on the mainland and Fleming, Diana, and Helby Islands. The dead-trapping transects provided data on shrews from these locations. In August 1977 scavenging invertebrates were sampled along single transects simultaneously for two nights on the three islands and at two locations on the mainland in areas with comparable habitat structure and composition. Each transect extended 100 m and contained 21 pitfall traps (plastic cups 10 cm deep, 7.5 cm diameter) baited with portions of mouse carcasses and arranged in a stratified random configuration.

Five individuals of each of the two most common species encountered in these pitfall traps (both large species of

Carabidae) were removed to the laboratory, and their feces were checked to insure that they were clear of ova. They were then fed infected livers from freshly killed deermice and their feces were examined daily for embryonated *C. hepatica* ova for the 10 days following.

Finally, behavioural interactions between these same carabid species and deermice were examined briefly in a Plexiglas arena (60 x 60 x 40 cm). Mice were deprived of food for eight hours and then introduced into the arena which contained a mouse carcass and three individuals of one beetle species. In six runs (three mice with each beetle species), all interactions were recorded for a 10-minute period immediately following introduction of a mouse.

Weather Monitoring

Weekly maximum-minimum temperatures in mature hemlock forest, approximately 30 cm above the forest floor, and monthly rainfall in adjacent open areas, were measured at three locations (Helby Island, Bamfield village, Mainland Live-Trap Plot 2) from 1 December 1976 to 7 October 1977.

RESULTS

Relative Abundance

Live-trap transects. Monthly captures of deermice along live-trapping transects from January 1976 to October 1977 are shown in Figure 2. Data from transect pairs are combined for each location. The number of captures varied among locations and within locations through time.

Monthly captures of adult males, adult females, all males, and all females from all five locations were ranked and tested by Kruskal-Wallis ANOVA (Marascuilo and McSweeney, 1977) for significant differences among locations. Multiple pairwise comparisons of confidence intervals (op. cit.) were used to determine the contrasts responsible for any significant H values from the ANOVA. Although monthly samples are not entirely independent, it was felt that this analysis might be useful to substantiate any apparent trends. Average numbers (from the 21 monthly samples) of adult males and of all males captured were similar on Haines and Diana Islands and at the two mainland locations, but were significantly ($p < 0.05$) lower on Helby Island than at all other locations (Table 2). Average numbers of adult females and of all females were similar on Diana Island and at both mainland locations, and were significantly greater ($p < 0.05$) than those on Helby Island.

Dead-trap transects (monthly). Total catch per unit effort (number of mice captured/number of adjusted trap nights) in monthly dead-trap samples from Helby, Diana, and Fleming Islands and from the mainland varied significantly ($p < 0.05$) within locations from month to month (Figure 3, Table 3). Total trapping success in the first six months exceeded that in the second six months in all locations, except Helby Island. Catch per unit effort for all months combined did not vary significantly among any of the locations (Table 4).

In order to detect any gradients in trap success due to "edge effect," individual transects from each location were divided into five consecutive groups of 10 trap points each, and catch per unit effort was calculated for each group. The t-test method of paired comparisons (Bailey, 1959) was then used to compare catches in the first 10 trap points (nearest to shore or roads) with catches in the second 10 trap points and in the fifth 10 trap points (farthest from shore or roads) from each location. In all locations except Fleming Island, catches were significantly higher in the first group than in either the second or the fifth group (Table 5). However, comparisons of the second and fifth groups revealed no significant differences at any locations. Any "edge effect" appears to be confined to the first 10 trap points.

Because of the "edge effect" apparent in three of the four locations, data from the first 10 trap points were excluded from the analyses in Figure 3 and Tables 3 and 4 for all locations.

Dead-trap transects (blitz). Catch per unit effort in dead-trap samples taken from 22 islands in Barkley Sound and from 10 locations on the adjacent mainland of Vancouver Island varied considerably among locations, but among the Barkley Sound islands there was no apparent relationship between island size and catch of males, of females, or of both sexes combined (Figures 4,5).

Total catch per unit effort from the 22 islands combined (344 mice/3225 adjusted trap nights) and total catch from the 10 mainland locations (112 mice/911 adjusted trap nights) did not differ significantly ($\chi^2 = 1.92$, $0.50 > p > 0.10$). However catch per unit effort of males was significantly ($p < 0.01$) lower on the islands (180/3144.5 a.t.n.) than on the mainland (74/892.5 a.t.n.) ($\chi^2 = 7.89$). Catch per unit effort of females did not differ significantly between mainland (36/873 a.t.n.) and island (164/3135.5 a.t.n.) samples ($\chi^2 = 1.76$, $0.50 > p > 0.10$).

These samples comprised almost exclusively reproductively active adults of both sexes. Therefore, abundance estimates from these samples should reflect densities of breeding populations.

Density Oscillations

Monthly live-trapping captures were examined for any differences in the amplitude of fluctuations among locations. Although monthly samples within a given location are not entirely independent, it was felt that a comparison of variances among locations was justified and would be useful to indicate possible differences.

Variances were tested for homogeneity by the F_{max}-test (Sokal and Rohlf, 1969), and were clearly heterogeneous (Table 6). Variances of adult male, adult female, total male, and total female numbers were highest on the mainland and lowest on Helby Island. Although the low values on Helby Island transects may be a function of relatively small means (at least in adult males, due to their approximate Poisson distribution), Haines Island and Diana Island variances were also relatively low. The data strongly suggest that through time these island populations may fluctuate less than the mainland populations. This conclusion is reinforced by the extensive heterogeneity observed in monthly dead-trap samples of mainland mice.

Reproduction

Reproductive activity. Reproductive activity varied both spatially and temporally within populations as well as among populations. In 1976 duration of breeding on the live-trap transects appeared to be shortest on the mainland, and shorter on the smallest island (Haines) than on either Helby or Diana Island (Figure 6). The data suggest that on all three islands reproduction may have continued with little interruption from the previous breeding "season," while on the mainland reproduction ceased during mid-winter. Data from the monthly dead-trap transects on Helby Island are very similar to those from the live-trap transects, but dead-trap data from Diana Island suggest a brief shut-down during March-April (Figures 7,8). Mainland dead-trap data show limited reproductive activity in mid-winter, and total inactivity only in the April sample.

In contrast to the variation in onset, duration, and cessation of breeding among live-trapped populations in 1976, the breeding seasons in 1977 varied little among these populations (Figure 6).

Breeding clearly ceased at all monthly live-trap and dead-trap locations during mid-winter 1976-77. In addition, the age structure and reproductive condition of animals caught during May-June 1977 in the dead-trap samples from 22 Barkley Sound islands indicated that no mid-winter breeding had occurred at any of those locations.

A comparison of the introduced populations in the Ross Islets revealed that mainland and island stocks did not differ appreciably in either timing or duration of reproductive activity (Figure 9).

Although there appeared to be some differences in the percentage of adults reproductively active on live-trap transects between the 1976 and 1977 breeding seasons, there were no striking differences between mainland and island populations within the breeding seasons in this respect. In both Ross Islets populations, adult participation in breeding was very high in males and females. During mid-breeding season, monthly dead-trap samples also revealed high adult participation at all locations. In the blitz dead-trap samples from 22 islands and the adjacent mainland, all adult males (n = 254) and all but six adult females (n = 186) were reproductively active.

Litter size. All litter size data were obtained from counts of embryos and of new placental scars from dead-trapped animals. Data from monthly dead-trap samples were analyzed by nested analysis of variance (locations nested by months). Litter sizes in mainland samples were significantly ($p < 0.01$) larger than those on Helby, Fleming, and Diana Islands, but litter sizes did not differ significantly ($p > 0.05$) among the three islands (Table 7).

To insure that lack of variation among months within individual locations was not simply due to small sample sizes, monthly samples were combined in three groups (April-July, August-October, November-March) and re-tested by analysis of variance for seasonal variation within locations. These analyses revealed no significant differences (Table 7).

Data from blitz dead-trap samples from 22 islands in Barkley Sound combined were compared by an unpaired t-test with those from adjacent mainland samples. Again, litters appeared to be smaller on the islands ($\bar{x} = 3.56$, $n = 159$) than on the mainland ($\bar{x} = 3.90$, $n = 29$), although differences were not quite significant ($t = 1.82$, $0.10 > p > 0.05$). Among Barkley Sound island samples, a regression of mean litter size on log island size revealed no apparent relationship between litter size and island size ($y = 3.66 - 0.07x$, $r = 0.01$).

Recruitment of Juveniles

Live-trap transects. Analyses of "juvenile" recruitment on live-trap transects include newly captured animals in either juvenile or sub-adult pelage. These categories were groups because of small sample sizes.

Nearly all juvenile male and female recruitment at both mainland locations was delayed until the end of the breeding season in 1976 and 1977 (Figure 10). In 1976 Haines Island males exhibited a peak similar to that of mainland animals, but in 1977 their recruitment was more dispersed over the latter half of the breeding season than in 1976 (Figure 10). Recruitment of juvenile females on Haines Island occurred throughout the breeding season in 1976, but in 1977 was limited to the latter half. On Helby and Diana Islands juvenile male and female recruitment fluctuated from month to month, but was dispersed throughout the breeding season at both locations.

Dead-trap transects (monthly). Percent composition of juveniles (in juvenile pelage only) in monthly dead-trap samples is shown in Figure 11. Males and females were grouped together because of their similar recruitment patterns at each location.

Mainland samples exhibited a recruitment peak at the end of the breeding season, which was similar to that found on the mainland live-trap transects. On Fleming Island a peak occurred in the latter half of the breeding season. Diana Island samples exhibited relatively low but steady recruitment throughout the breeding season. Recruitment in Helby Island samples was similarly dispersed, but fluctuated from month to month.

Despite differences in duration of breeding activity among locations, the relative abundance of juveniles for all months combined did not differ significantly among the four locations ($\chi^2 = 7.67$, $0.10 > p > 0.05$). However, the data suggest that Helby Island samples contained more juveniles (11% of total catch) than Diana Island (5%), Fleming Island (6%), or mainland (6%) samples.

Ross Islets. Recruitment in populations introduced to the Ross Islets derived from island and mainland stocks was similarly dispersed throughout the breeding season in both populations (Figure 12). The pattern of recruitment in the mainland stock clearly differed from that observed in populations on the mainland live-trap and monthly dead-trap transects.

Agonistic Behaviour

All social interactions recorded in the arena experiments were arranged in four major categories of behaviour: approach, investigatory, cohesive, and agonistic (Table 8). In each category individual scores (number of social interactions in each encounter) were ranked and examined for differences among locations by Kruskal-Wallis analysis of variance (Table 9). Analyses were carried out in which mainland locations were considered both separately and combined.

The mean frequencies of approaches did not differ significantly between locations. Although investigatory behaviours (nasonasal, nasoanal, and other body sniffing) appeared to vary in frequency between locations, no differences were significant ($0.10 > p > 0.05$).

Cohesive behaviours (huddling, allogrooming) were uncommon, but were significantly ($p < 0.05$) more frequent in mice from Diana Island than in those from Helby and Haines Island. They occurred during four encounters in animals from Diana Island and during two encounters in animals from Mainland 2, but were absent in animals from all other locations.

Agonistic behaviours (aggressive and defensive combined) were relatively common in animals from all locations. Mean frequencies of agonistic interactions in mainland animals (8.4) were very similar to those in Diana Island animals (8.6), but appeared to be lower than mean frequencies in animals from Helby (12.6) and Haines (14.0) Islands ($0.10 > p > 0.05$). Defensive behaviours (avoidance, defensive uprights, submission, flight, and escape leap) did not appear to differ between any locations ($0.50 > p > 0.10$), and made up the majority of agonistic behaviours in mice at all locations. In contrast, the frequency of aggressive behaviours (attack leap, side display, chasing, fighting, boxing, threat, rush, and bite) varied very significantly ($p < 0.005$) among locations. In the analysis with Mainland 1 and 2 combined, animals from the mainland and from Diana Island exhibited similar and relatively low mean frequencies (0.9, 0.8) of aggressive interactions. Mice from Haines Island ($\bar{x} = 3.9$) were significantly ($p < 0.05$) more aggressive than mainland and Diana Island mice, while those from Helby Island

($\bar{x} = 2.5$) appeared to occupy an intermediate position between Haines Island and mainland-Diana Island animals.

The mean frequencies of all social interactions combined did not differ significantly between any locations. In Haines and Helby Island mice 64.2% and 71.2% of all interactions observed were agonistic; in contrast, only 49.7% of interactions in Diana Island mice were agonistic.

Avoidance was the most frequently observed agonistic behaviour in mice from all locations. Defensive uprights were second in frequency, but were less common in mainland mice (13 occurrences/20 encounters) than in Diana (17/10), Helby (18/10), or Haines (26/10) mice. Fights and bites occurred infrequently, and were observed only in island animals. Tooth chattering and foot pattering were observed in mice from all locations. Although they were not quantified, these behaviours appeared to be especially prevalent in Haines and Helby mice.

Tail Wounding

Mice with tail wounds were frequently observed in live-trap and dead-trap samples from all locations. In contrast to body wounds (and scars), tail wounds are easy to observe in live-trapped animals in the field; thus, wounding levels in live-trapped and dead-trapped animals can be compared. Mice from all samples were assigned to one of four levels of tail wounding based on its extent and severity: nil, light, moderate, severe. Animals with 1-2, 3-4, and greater than four distinct wounds (or scars) were generally assigned to light, moderate, and severe levels respectively.

Live-trap transects. In live-trapped animals, tail wounds appeared to heal very quickly. On several occasions mice were trapped with severe wounds one month and with no visible wounds the following month. Rapid wound healing is also reported in meadow voles (Rose and Heuston, 1978). With the assumption that most wounds seen are acquired in the monthly trapping interval, it is possible to combine monthly samples within locations.

Monthly samples were combined and arranged into breeding and non-breeding seasons. A breeding season was arbitrarily defined by >10% of adults being reproductively active. Samples from the first month following a breeding season were included with those from the breeding season to allow for wound healing.

The 1976 and 1977 breeding seasons were considered separately, but due to small sample sizes on the islands all non-breeding samples were combined in one non-breeding season. χ^2 analyses were performed on adult males and females separately to detect any differences in wounding levels between breeding and non-breeding seasons, and between the 1976 and 1977 breeding seasons at each location. Analyses were also performed to detect any heterogeneity among locations in both breeding and non-breeding seasons.

In addition, adult males and females were compared at each location during breeding and non-breeding seasons. Although the statistical assumption that monthly samples are entirely independent was not met, it was felt that the χ^2 analyses might be useful to indicate any trends in the data.

Males showed very significantly ($p < 0.005$) higher levels of tail wounding than females at all locations during the 1976 breeding season, and at all locations except Helby Island during the 1977 breeding season (Table 10). In the non-breeding season Haines Island, Diana Island, and Mainland 2 males also showed significantly ($p < 0.025$) higher levels of wounding than females, but Mainland 1 males and females did not differ significantly ($0.10 > p > 0.05$).

Comparisons of wounding levels within and among locations are summarized in Table 11. In Haines Island males, levels were higher in both breeding seasons (B_1,B_2) than in the non-breeding season (NB). In Helby and Diana Island males, levels did not differ significantly between breeding and non-breeding seasons. In both mainland locations B_1 and NB levels were similar, but B_2 levels exceeded NB levels. In Helby Island males B_1 levels exceeded B_2 levels, but at all other locations the converse was true.

In Haines and Diana Island females, wounding levels were higher in NB than in B_1 but did not differ between

NB and B_2. In Mainland 1 females neither B_1 nor B_2 levels differed significantly from NB levels, but in Mainland 2 females NB levels were greater than B_1, but less than B_2 levels. At all locations except Diana Island there was significantly greater wounding in the 1977 breeding season than in the 1976 breeding season.

Among males, wounding levels in all seasons (B_1,B_2, NB) were significantly higher on Haines Island than on the mainland (Table 11). Levels were highest on Helby Island in B_1, but in B_2 and NB levels on Helby Island were intermediate. In all seasons wounding levels were intermediate on Diana Island, and lowest on the mainland.

Among females wounding levels were highest on Haines and Helby Islands in B_1 and B_2. Levels were relatively low on Diana Island and on the mainland in these seasons, although in B_2 Diana, Mainland 1, and Mainland 2 samples all differed significantly. In NB no significant differences among locations were detected.

In most locations tail wounding was primarily restricted to adults, and occurred rarely in young (juvenile and sub-adult) mice of either sex (Table 12), except Haines males.

Dead-trap transects (monthly). Tail wounding levels in adult mice from monthly dead-trap samples were combined, and the totals were compared among locations by Kruskal-Wallis analysis of variance (Table 13). In males there was highly significant ($p < 0.001$) variation among locations, with lowest levels on the mainland, intermediate levels on Fleming and Diana Islands, and highest levels on Helby Island. The multiple confidence intervals procedure used did not account for ties, and significance levels in comparisons between locations are therefore conservative.

In females, variation among locations was much smaller than in males, although wounding levels on the mainland were significantly ($p < 0.05$) lower than those on Helby Island.

At all locations wounding levels were clearly higher in males than in females, although differences were more striking in island than in mainland locations.

Again, wounding occurred rarely in young (juvenile and sub-adult) mice of either sex at any location.

Dead-trap transects (blitz). Combined tail wounding levels in adult male mice from dead-trap samples collected on 22 islands were significantly ($p < 0.01$) higher than levels in males from adjacent mainland samples (Table 13). However, there was no difference between island and mainland females. A comparison of males and females showed no significant difference in mainland samples, and significantly ($p < 0.001$) greater levels in island males than in island females.

Partial correlation analyses of samples from the 22 islands revealed, with the effects of age removed, weak but significant negative correlations between wounding levels and the log of island size in male mice ($r = -.148$, 168 d.f., $p = 0.022$) and female mice ($r = -.240$, 155 d.f., $p = 0.001$).

Ross Islets. Subject to the same statistical limitations as samples from the monthly live-trapping transects, wounding levels in adult mice were compared by χ^2 analyses to detect differences between introduced mainland and island stocks (Table 14). Males and females in the Helby Island stocked population experienced significantly higher levels of wounding than those in the mainland stocked population.

Adult Immigration

Adult immigration rates (number of unmarked adults/ total number of captures) on live-trapping transects were calculated for each monthly sample. At all locations there was an apparent relationship between reproductive activity and adult immigration in both sexes (Figures 6,13). In males, with the cessation of breeding immigration clearly declined at all locations. A recognizable peak at the onset of breeding was found at Mainland 1 (1976 and 1977), Diana (1977), and Helby (1977), but was lacking at Haines and Mainland 2. In females the pattern was generally similar, although recognizable peaks of immigration at the onset of breeding were found only at Helby (1977) and Mainland 1 (1976). In a majority of months at all locations, adult male immigration rates exceeded adult female rates.

Any peaks in adult immigration in the first several months of the study must be interpreted cautiously, due to the possibility of low trap success during this period.

Mortality

Survival. Survival (number of mice captured in month n known to be alive in month n+1/total number of mice captured in month n) on live-trapping transects was calculated for each monthly sample. In both sexes at all locations, survival fluctuated widely from month to month, but no pattern or relationship with breeding season was discernible (Figures 6,14). The data from each location and each sex were subjected to runs tests for trend data (Sokal and Rohlf, 1969) and there was no significant departure from a random trend in survival in any group.

Mean survival was calculated for each group (Figure 15). Among males survival appeared to be lower on Helby Island than on Diana Island or the mainland, but among females there were no apparent differences between any groups.

Survival data were examined for correlation with adult immigration by calculating correlation coefficients of survival at month n and adult immigration rate at month n+1. Survival and adult immigration were independent in all groups except Mainland 2 females, in which there was a weak but positive correlation ($r = 0.49$, $p < 0.05$).

Length of life on live-trapping transects. An alternate method of assessing survival in live-trapped populations is to measure the time an individual is known to be alive.

Length of life on live-trapping transects was calculated for all animals captured before June 1977, and is arrayed for all locations by age (juvenile-sub-adult or adult) at first capture in Figures 16,17. These data were ranked and compared among locations by Kruskal-Wallis analysis of variance (Table 15).

In males and females first captured as adults, and in females first captured as juveniles-sub-adults, there were no significant differences in length of life on traplines between any locations. However, in males first captured as juveniles-sub-adults, the average length of life was significantly ($p < 0.05$) shorter on Helby Island than on the mainland.

From these data it is impossible to separate mortality and emigration components. Among male mice first captured as juveniles-sub-adults, a relatively small proportion of mainland animals (7%) in comparison to island animals (23%) were trapped in only one month. Among mice first captured as adults, individuals that were trapped in only one month were likely transients. With this assumption, the proportions of transients in adult captures were compared by χ^2 among locations for each sex, and within locations between sexes, and no significant differences were detected in any group. There appeared to be no difference in the degree of transience in adults between sexes or among locations.

Age distribution. Age distributions of deermice from dead-trap samples are shown in Table 16. Monthly samples represent catches from all months combined.

Distributions from these combined monthly transect samples were analyzed by Kruskal-Wallis analysis of variance. Males on Helby and Fleming Islands were significantly ($p < 0.05$) older than those on Diana Island and the mainland. There were no differences between females from any location.

Age distributions in blitz dead-trap samples from the mainland and from all islands combined were compared by χ^2. Old males formed a significantly ($p < 0.05$) greater proportion of the population on islands than on the mainland, but there were no apparent differences between island and mainland females. Among the islands, a weak but significant negative correlation between age and log of island size in males (Pearson r = 0.141, d.f. = 179, p = 0.03) suggests that age structures of males may be more top-heavy on small islands than on large islands. Comparisons between sexes revealed that on islands (all combined) males were significantly ($p < 0.01$) older than females ($\chi^2 = 14.31$), while on the mainland there was no apparent difference in age structure ($\chi^2 = 0.49$) between the sexes.

Sex ratio. Sex ratios from monthly dead-trap samples were examined in each age group and for all age groups combined. They were compared by χ^2 for heterogeneity among locations, and by χ^2 for goodness of fit to 1:1 within locations (Table 17). There were no significant differences in sex ratios between locations. When all age groups were combined there appeared to be more males than females at all locations, although the ratios deviated significantly from 1:1 only in mainland and Diana Island samples. Analysis by age group revealed significant deviations in favour of males in Diana Island age group 1-2, mainland age group 3, and Fleming and Diana Island age group 4.

Unfortunately it is impossible to determine whether changes in sex ratio with age reflect different mortality rates or simply reflect changes in relative trappability.

Embryo resorption. Embryo resorption was uncommon in both monthly and blitz dead-trap samples (Table 18). In monthly samples resorption frequency was significantly ($p < 0.01$) greater in mainland mice than in island mice (Helby, Diana, and Fleming Islands combined), but in biltz samples no significant difference was detected between mainland and island mice. However, within the latter, resorption was significantly ($p < 0.01$) more common on the relatively small islands (<33 ha) than on the relatively large islands (>45 ha) (Table 19).

Mortality in young mice. From the monthly dead-trap samples, it was possible to estimate the survival of juveniles to subadulthood in populations by comparing at each location captures of age 1-2 animals in juvenile pelage and captures of age 1-2 animals not in juvenile pelage (Table 20). It was felt that this estimate would be relatively free of bias by differences in duration of breeding between locations. Based on this estimate, survival of juveniles to sub-adulthood was lower on Helby Island than at all other locations.

Survival of recruits to the introduced populations in the Ross Islets was examined by comparing the numbers of recruits from 1977 known to be alive and the numbers not known to be alive at the final trapping rota (Table 21).

Based on this estimate, survival of all recruits, and of male recruits alone was significantly ($p < 0.025$) lower in the Helby population than in the mainland population, but survival of female recruits alone did not differ significantly between the two populations.

Cannibalism. Direct evidence of cannibalism (= intraspecific predation) was lacking in all populations, and it is difficult if not impossible to collect such data in the field. However, initial observations of necropsied animals revealed that infection levels of the parasitic nematode *Capillaria hepatica*, which has been used as an indirect indicator of cannibalism in other deermouse populations (Freeman and Wright, 1960), were unusually high in the island populations from Barkley Sound.

Therefore an attempt was made to determine the usefulness of *C. hepatica* as an indicator of cannibalism in the study populations. This required not only an examination of the prevalence and severity of *C. hepatica* infections in these mice, but also the roles which predators and scavengers might play in the distribution of the parasite.

Capillaria hepatica

Modes of transmission. *Capillaria hepatica* occurs as an adult in the liver of its host, where it deposits its eggs and eventually dies. Infective ova are generally not passed in the feces of the host, but are released from the liver through cannibalism, predation, necrophagy, or possibly natural death and decomposition (Freeman and Wright, 1960). The last mode, however, may reduce the viability of eggs (op. cit). They may be ingested subsequently by a host directly through coprophagy or from contaminated soil or nesting material (Figure 18).

Location differences in infection. The presence and severity of *C. hepatica* infections in mice from the monthly dead-trap transects are summarized in Table 22. Prevalence was highest (74%) on the smallest island (Helby), intermediate (52%, 51%) on Diana and Fleming Islands, and lowest (16%) on the mainland of Vancouver Island. The number of severely damaged livers was highest on Helby Island, but did not differ greatly among other locations.

Prevalence and severity data from mice collected during the blitz dead-trapping on 22 islands and the adjacent mainland are summarized in Table 23. Once again prevalence was higher on the islands (80%) than on the mainland (37%), but the severity of infections (with all islands considered as a single group) was quite similar. Among the islands themselves there was a highly significant negative correlation between island size and the prevalence and severity of *C. hepatica* (Kendall's Tau = -0.146, $n = 327$, $p < 0.001$).

Effects of age and sex on infection. In Table 22, levels of infection increased with age in animals from all locations, although on Helby Island increases after age 3 were not statistically significant. When the samples are arrayed by age group the same relationships shown among locations by total groups generally remain, with highest prevalences on Helby Island, intermediate prevalences on Diana and Fleming Islands, and lowest prevalences on the mainland. In Table 23 island mice showed consistently higher levels of infection than mainland mice in each age group.

C. hepatica infections from Tables 22 and 23 were divided by sex and tested by χ^2 for differences in levels of infection between males and females. The analysis revealed no significant differences between levels of infection in males and females for any age group in any location.

Seasonal differences in infection. The cumulative nature of *C. hepatica* infections makes detection of seasonal changes in infection rate difficult. However, if there is a seasonal pattern of infection it should reveal itself in an analysis of infections in very young animals. Infection data from Table 22 for age group 1-2 were divided into five seasons (March-April, May-June, July-August, September-October, November-January). Arrangement by seasons effectively increases sample size by lumping data from months which are similar climatically and/or biotically. These were analyzed by Kruskal-Wallis analysis of variance for heterogeneity among seasons for each location and were significant only on the mainland ($H = 11.41$, $p < 0.025$). However, mean ranks from the Kruskal-Wallis ANOVA showed similar seasonal patterns among all the locations (Figure 19). Locations were subsequently lumped and the data showed significant heterogeneity among seasons ($H = 12.47$, $p < 0.025$) with lowest infection levels in July-August and highest levels in November-January.

Other parasites. Exclusive of several large cysts which may have contained metacestode larvae, livers from deermice in the present study were infected with metacestodes of only one genus, *Mesocestoides*. These helminths were found both encysted in the liver and free in the peritoneal and pleural cavities. The prevalence of *Mesocestoides* sp. varied considerably among locations, but was consistently lower than that of *C. hepatica* (Tables 22 and 23). *Mesocestoides* sp. differed fundamentally from *C. hepatica* in two ways: its distribution was spatially patchy, and it was significantly more common in females than males (48/760 vs. 32/963, $\chi^2 = 7.76$, $p < 0.01$).

Role of scavengers. In the present study two species of large ground beetles, *Scaphinotus angusticollis* and

Pterostichus lama, as well as shrews and deermice were occasionally observed feeding on carcasses of trap-caught mice. *S. angusticollis* and *P. lama* were the dominant species in pitfall traps (Table 24). Due to their large size relative to other species encountered, a simple numerical analysis probably underestimates their dominance as scavengers. When considered together these two species were similarly abundant on the three islands (Helby, Diana, and Fleming), and significantly ($p < 0.05$) less abundant on the islands than on the mainland. Shrews were occasionally caught in break-back traps during mouse trapping. They were entirely absent from Helby Island, but were similarly abundant on Diana and Fleming Islands and significantly ($p < 0.005$) more abundant on these two islands than on the mainland (Table 24). The use of break-back traps is a relatively inefficient capture technique for shrews and the very low catch figures for shrews probably underestimated abundance. However, they should provide an acceptable measure of relative abundance.

In the laboratory *S. angusticollis* and *P. lama* were fed mouse livers infected with *C. hepatica*. Examination of a sub-sample of these livers revealed ova in predominantly one-celled and rarely two-celled stages. *P. lama* began passing unembryonated ova 48 hr after ingestion, four- and eight-celled ova 72 hr after, and by 120 hr ceased passing all ova. However, *S. angusticollis* freely ate infected livers but passed no ova at all. The tribe Cychrini, to which the latter species belongs, is known to practice pre-oral digestion (Thiele, 1977) and *C. hepatica* ova were probably destroyed before they were even ingested.

Deermice which had been deprived of food for 8 hr were introduced for 10 min into an arena which contained a mouse carcass and three *P. lama* or three *S. angusticollis*, in order to examine general behavioural interactions and specifically to determine whether mice would attack and ingest beetles. In all six runs mice showed a keen interest in the carcasses. When they approached the beetles, both *S. angusticollis* and *P. lama* responded by raising the tips of their abdomens and releasing a volatile secretion. In all cases mice quickly retreated. If the beetles were disturbed while feeding on a carcass they simply released their defensive secretion and resumed feeding; this behaviour effectively denied mice access to carcasses as long as beetles were present on or near them.

Morphological Comparisons

Weight. In monthly dead-trap samples mean weights of mainland mice (both sexes) were lower than those of island mice in most age categories (Figure 20). Of the three island populations, in age classes 3, 4, and 5-6 Helby Island males were significantly heavier than Diana and Fleming Island males. A similar pattern was seen in females; although in age class 5-6 the differences were not significant. Unfortunately, sample sizes of island females in this age category were relatively small.

In Helby and Diana Island males, and in Helby Island females, mean weights increased rapidly between age classes 2 and 3. This suggests that more rapid growth occurs in this age interval in these populations than in the other populations. However, these data should be interpreted cautiously, because samples for each age class contain different individuals. In addition to growth, differential survival of individuals that differ in weight could affect the relationship between age and body size.

At all locations there were no significant differences between mean body weights of males and females in any age class.

A comparison of body weights among the 22 islands sampled in Barkley Sound during the blitz dead-trapping revealed an apparent negative correlation with log of island size in males and females (Figures 21,22). However, there was considerable variation among locations. Despite significant correlations in males ($r = -0.214$, d.f. = 179, $p = 0.002$) and females ($r = -0.297$, d.f. = 159, $p < 0.001$), slopes of both regressions did not differ significantly from zero. Age differences were likely responsible for some of the natural variation, although partial correlation analysis with age controlled, produced r- values very similar to those above.

There was also an apparent relationship in males between body weight and abundance (catch per unit effort). The correlation was weak but significant, and remained so during partial correlation analysis when the variables log island size, tail wounding, and age (alone and in all possible combinations) were controlled ($r_{\text{abund wt. isld size twound age}} = 0.204$, d.f. = 166, p = 0.004).

Body-tail ratio. In monthly dead-trap samples ratios of body length to tail length were clearly lower in mainland animals than in island animals (Figure 23). In other words, mainland mice had relatively longer tails (in relation to body length) than island mice. Ratios from the three islands were generally similar to one another.

There were no apparent differences between sexes and very few apparent differences between ages at any location.

Among the blitz dead-trap samples body length/ tail length ratios in island mice from Barkley Sound varied from island to island, but were consistently greater than those in mice from the adjacent mainland (Figure 24). Ratios in mainland mice also varied from location to location. There was no indication that the variation among islands was related to island size or to relative proximities of islands.

Vegetation

Vegetational comparisons among the permanent live-trapping transect areas revealed only minor differences (Table 25). Western hemlock (*Tsuga heterophylla*) overwhelmingly dominated the canopy at all locations. The understory and shrub layers at all locations were most commonly open or dominated by salal (*Gaultheria shallon*). On the mainland red huckleberry (*Vaccinium parvifolium*) and on the islands evergreen huckleberry (*V. ovatum*) were also common.

There were no striking differences between mainland and island locations in the amounts of deadfall material present.

Weather

Mean monthly temperature maxima varied by only 0.8°C among locations, but the mean monthly minimum was 1.9°C and 2.5°C higher on Helby Island than at the two mainland locations (Table 26). Mean monthly temperature fluctuations (monthly maximum minus monthly minimum) were lowest on Helby Island. The highest monthly minimum and lowest monthly maximum were also recorded on Helby Island.

Total precipitation for the 10-month sampling period varied from 162 cm on Helby Island to 205 cm on Mainland 2.

DISCUSSION

Abundance and Density Oscillations

Abundance estimates based on trap success from removal trapping are necessarily crude. Despite the limitations of this technique for census purposes in general (for a good discussion see Grant, 1962) and on islands in particular (Webb, 1965) I feel that comparisons among areas of similar habitat from trappings of consistent effort and brief duration can yield a useful index of relative density.

In this study island and mainland densities did not differ consistently. Densities appeared to be higher on some islands than others, and appeared to vary from place to place on individual islands, but there was no relationship with island size. This variability suggests a need for caution in generalizing about island patterns from intensive studies of only a few islands. Although the "fence effect" (Krebs et al., 1969) may be operating on some islands, it does not appear to be widespread in this island group.

Actually, with all islands grouped, densities of breeding males in 1977 appeared to be lower on the islands than on the mainland. Webb (1965) reported lower densities of *P. maniculatus* on very small islands in Adirondack lakes than on the adjacent mainland, and McCabe and Cowan (1945) found very low densities of *Peromyscus* sp. in the interior of islands along the northern British Columbia coast. Insular populations of *Apodemus sylvaticus*, an ecological equivalent of *P. maniculatus*, were generally lower on small islands than on the adjacent British mainland (Delany, 1961).

Unfortunately, mainland and island habitats frequently differ, and therefore availability of food may differ between them. Sullivan (1977) implicated abundant food as one factor in maintaining high population densities of *P. maniculatus* in one of his Gulf Island study areas. Supplemental feeding experiments have increased densities in *Peromyscus leucopus* (Bendell, 1959), in *Apodemus sylvaticus* (Flowerdew, 1972), and to a limited extent in *Peromyscus maniculatus* (Fordham, 1971). Although no attempt was made in the present study to measure food availability, vegetational structure and composition on the islands and on the adjacent mainland were quite similar.

Beach and adjacent supralittoral "edge" habitats often provide abundant food for coastal and island deer-mice (Foster, 1965). This relative abundance of food was likely responsible for the generally increased numbers of mice near the shore in the present study. Although the "edge effect" disappears within 100 m of shore, it could substantially increase overall densities on small islands. In island studies where most trapping is conducted close to shore, density estimates could be inflated.

Redfield (1976) predicted that the variance in population size of *P. maniculatus* should be lower on islands than on the mainland, since this would keep island populations as far from extinction as possible. This appears to be true at least on some islands in Barkley Sound. Relatively high variance on the mainland may partially reflect more variable trap success due to the slightly more rigourous winter environment on the mainland than on the islands, although there is little evidence of this.

Reproduction

Although fluctuations in island populations were relatively small, reproductive activity on the islands clearly differed between 1976 and 1977. Sadleir (1974) found major year to year fluctuations in onset, cessation, and intensity of breeding in west coast *P. maniculatus*, but noted that in each year seasons were generally synchronous in different forest habitat types. Although reproductive activity was generally synchronous on island, mainland, and Ross Islets live-trap plots in 1977, there were clear differences between island and mainland locations in 1976. At this time island populations showed extended breeding, similar to that reported by Sullivan (1977) in Gulf Island *P. maniculatus*. In addition, differences in intensity of breeding in live-trap and dead-trap samples in some months suggest that local variation occurs on individual islands and on the mainland.

A separate early breeding peak, as described by Fairbairn (1977) in coastal deermouse populations on mainland British Columbia, was not apparent at any locations in the present study.

If energy availability, through a combination of food supply and temperature, limits reproduction in west coast deermice (Sadleir et al., 1973), one might conclude that available energy differed between 1976 and 1977, and also that in 1976 energy regimes on the mainland and on the islands differed.

Although high density has been implicated in the early cessation of breeding in a northern Alberta population of *P. maniculatus* (Canham, 1969), Sadleir (1974) found no relationship between breeding and population density in west coast deermice. In the present study Ross Islets populations probably reached the highest densities, but resembled all other populations in their breeding activity.

In 1976 litters were smaller on the islands than on the mainland. Unfortunately, in 1977 the sample of mainland females was small, but mainland litters were still apparently larger than island litters. There was also an apparent decrease in average litter size from 1976 to 1977 at island and mainland locations.

Millar (1977) considers litter size and the time to weaning to be "the adaptive variables of mammalian reproduction." Although the size and number of offspring, and the length of the breeding season all contribute to the reproductive effort and therefore the energy requirements of a female, he stresses that energy limits may not always be important in the evolution of reproductive rates.

Accurate estimates of reproductive effort are obviously lacking in the present study. Precise measurements of age and size at weaning and of growth rates in mainland and island animals would be useful in this regard. It appears that effort on the islands may fluctuate considerably from year to year; nevertheless, population size appears to remain relatively constant. This contrasts with Bujalska's (1973) observations of an insular *Clethrionomys glareolus* population in which total female reproductive effort remained relatively constant from year to year, but population numbers varied. Although Redfield (1976) suggested that Gulf Island deermice may reproduce less intensively than their mainland counterparts, there is no consistent indication of this in Barkley Sound deermice.

Juvenile Recruitment

Recruitment patterns of young animals varied temporally and spatially. The dispersion of recruitment throughout the breeding season on Helby and Diana Islands, and to a limited extent on Haines Island resembled that observed by Sullivan (1977) in Gulf Island deermice. Mainland populations, with a major peak of recruitment at the end of the breeding season, resembled coastal populations in mainland British Columbia (Sadleir, 1965; Petticrew and Sadleir, 1974; Fairbairn, 1977).

Slight discrepancies in juvenile recruitment between mainland live-trapping and dead-trapping transects suggest that some juveniles may be present before the end of the breeding season, but are less trappable in live-traps than in dead-traps at this time. These discrepancies have also been noted by Sadleir (1970).

Delayed recruitment in mainland populations has been attributed to agonistic behaviour of breeding males toward juvenile males and females (Sadleir, 1965, 1974; Healey, 1967). Halpin and Sullivan (1978) attributed the dispersed recruitment of juveniles in Gulf Island deermice to the low levels of aggression that they observed in breeding males from those populations.

Although juvenile recruitment patterns of Gulf Island and Barkley Sound island populations are apparently similar, levels of agonistic behaviour in breeding males appear to differ. Arena experiments on Barkley Sound deermice demonstrated significant differences in cohesive and aggressive behaviours between islands. Of the three islands sampled, mice were most aggressive on the smallest (Haines), and least aggressive and most cohesive on the largest (Diana). Diana mice and mainland mice did not differ in cohesiveness or aggressiveness; nevertheless, they exhibited entirely different juvenile recruitment patterns.

Aggression and Wounding

The general correlation among locations between aggressiveness in arena experiments and tail wounding levels on live-trap transects suggests that tail wounding may be a useful index of aggressiveness in Barkley Sound populations. Differences in wounding between breeding seasons in some locations suggest that aggressiveness may not only fluctuate seasonally, as reported by Sadleir (1965) and Healey (1967), but may also fluctuate from year to year.

Tail wounding was generally confined to adults; only in Haines Island males was there extensive wounding of young animals.

Wounding levels in dead-trap samples were higher in island males than in mainland males. Among locations sampled monthly, Helby males were most severely wounded and mainland males were least wounded. Among the

22 islands sampled during 1977, wounding levels in males appeared to increase as island size decreased.

Tail wounding in females is difficult to interpret. Although wounding levels were relatively low in comparison to male levels at most locations, they increased at all locations except Diana Island between 1976 and 1977. It is unknown whether these wounds result from intra- or intersexual encounters. Wounding levels in Haines and Helby females were generally higher than those in mainland females. Unlike levels in males, levels in females were not consistently greater during breeding than during non-breeding.

Wounding and scarring are rarely observed in *P. maniculatus* (Krebs, pers. comm.). They also occur rarely in *Peromyscus polionotus* (Ramsey, 1973 as cited by Garten, 1976), although overt aggressive interactions have been observed in insular populations of that species (Blair, 1951).

Ross Islets Introductions

The responses of island and mainland populations to introduction to the Ross Islets were interesting in several respects. Although "colonization" may stimulate breeding in introduced populations of *P. maniculatus* (Sheppe, 1965), this response did not occur in Ross Islets populations. In both stocks there was a five-month lag between introduction and the onset of breeding, which was generally synchronous with the onset of breeding on mainland and island live-trapping transects.

Levels of aggressiveness in the introduced populations, based on tail wounding indices, were lower in the mainland stock than in the Helby Island stock. Juvenile recruitment in both populations was dispersed throughout the breeding season. This suggests that the mechanism that normally delays juvenile recruitment in mainland populations was not operating in the introduced mainland population. Sadleir (1965) and Healey (1967) argued that breeding males on mainland British Columbia prevent recruitment of juveniles by forcing them to disperse into sub-optimal habitat, rather than by actually killing them. In sub-optimal habitat juveniles may suffer high mortality due to decreased energy availability and/or increased predation. Small islands usually lack these dispersal "sinks"; as a result, juveniles from mainland stocks introduced to them might successfully recruit throughout the breeding season. Alternatively this recruitment pattern may only be an artefact of the introduction.

How have island populations adjusted to lack of a dispersal sink? A partial solution is to minimize the production of surplus animals, although in any habitat it is wise to produce some. If surplus individuals cannot be removed by forcing them to disperse, perhaps they succumb to more direct intraspecific mortality factors. In the Ross Islets populations, despite similar recruitment patterns, survival of recruits was significantly lower in the Helby stocked population than in the mainland stocked population.

These introduction experiments should be interpreted cautiously, and can be criticized because they were not replicated, and because they were carried out on islands smaller than those that support natural populations of deermice in Barkley Sound. However, it seems clear that there were differences between mainland and island mice exposed to similar environments.

Mortality

Mortality patterns frequently differ between island and mainland populations (Kramer, 1946; Tamarin, 1977a, b,c; Case, 1978; Heaney, 1978). Krebs et al. (1969) and Bujalska (1975) noted the relative importance of juvenile mortality in determining the size of enclosed and insular vole populations.

In the present study, fluctuating preweaning mortality rates were likely important in maintaining the low population variance on islands in the face of fluctuating reproductive effort.

Embryo resorption did not appear to be an important mortality factor in island or mainland populations. Sadleir (1974) also reported very low pre-natal mortality rates in west coast deermice. Although Coutts and Rowlands (1969) and Tamarin (1977a) observed higher resorption rates in insular voles than in mainland voles, there were no consistent differences between mainland and island losses in the present study. However, among Barkley Sound islands in 1977, resorption was more common on small islands than on large islands.

It is often difficult to determine the fate of young in small mammal populations. Unfortunately I do not have an accurate estimate of mortality between birth and the age when animals first enter traps, because I used a monthly rather than semi-monthly trapping schedule in order to sample more localities. However, mortality during this interval was apparently high at all locations, particularly on the islands in 1976, where, despite prolonged and intensive breeding, recruitment of young was very low.

Based on the monthly dead-trapping samples in 1976, survival of juveniles to sub-adulthood varied among locations. Although it was similar on Diana and Fleming Islands and the mainland, it was relatively low on Helby Island. Relatively low survival was also observed in 1977 in the Helby Island stock introduced to the Ross Islets.

In addition, the average stay of individual mice on the monthly live-trapping transects was significantly shorter among males first captured as juveniles-subadults from Helby Island compared with those from the mainland. Haines and Diana Island values were intermediate between Helby Island and mainland values. These differences may reflect differences in mortality or differences in mobility among the populations. In contrast males and females first captured as adults displayed little difference among locations in average length of stay on the traplines.

Mazurkiewicz and Rajska (1975) suggested that in insular *Clethrionomys glareolus* old adults play an important role in population processes by occupying optimum habitat and excluding young animals. Foster (1965) and Redfield (1976) noted increased longevity and top-heavy age distributions in insular *P. maniculatus* populations. In Barkley Sound age distributions of male mice were top-heavy on most but not all islands sampled. This tendency generally increased as island size decreased. In contrast, female age distributions differed little among islands, or between islands and mainland.

Animals and plants on islands frequently live longer than their mainland counterparts, since predation and interspecific competition pressures on islands are often relaxed (Carlquist, 1974). In Barkley Sound, island males that survive the initial period of heavy mortality in early life are likely to live longer than their mainland counterparts. However, island females do not live longer than mainland females. Different mortality factors appear to be operating on males and females.

Sex ratios in natural and laboratory populations of *P. maniculatus* generally favour males (Terman and Sassaman, 1967). Canham (1970) reported decreased proportions of males in declining populations of boreal deermice, and Hoffmann (1955) observed ratios favouring females in an unusually high population of California deermice. Island populations might be expected to support larger proportions of males than mainland populations, since this would inhibit rapid population growth (Myers and Krebs, 1971; Tamarin, 1977b); but there is no evidence of this on Barkley Sound islands.

Potential mammalian predators of deermice on the mainland of Vancouver Island include weasels (*Mustela erminea*), marten (*Martes americana*), and mink (*Mustela vison*). In addition, shrews (*Sorex obscurus*) may prey on untended young in the nest although I am unaware of any published accounts of this. Mink are abundant on islands in Barkley Sound but weasels and marten are absent (Guiguet, 1974). In an analysis of more than 1000 mink scats from the Barkley Sound area (islands and mainland) Hatler (1976) found remains of *P. maniculatus* in only one. However, the prevalence of

Mesocestoides sp. in island mice suggests that predation by some mammal, probably mink, occurs on some islands (Holmes, pers. comm.).

Screech owls (*Otis asio*) are the only common effective avian predators of deermice in the Barkley Sound area and occur in low but similar densities on the islands and the adjacent mainland (Hatler, pers. comm.). Deermice form the major portion of the diet of screech owls in many other areas (Craighead and Craighead, 1956).

Cannibalism is an obvious potential source of mortality in an enclosed or insular population in which interspecific predation pressure is reduced. Cannibalism of young by adults is common in insular populations of wall lizards, *Lacerta sicula*, in the Adriatic, although it is rare in adjacent mainland populations of the species (Kramer, 1946). Holmes (1977) observed cannibalism in arctic ground squirrels during escalated territorial disputes, and noted a positive correlation between its frequency and population density. Cannibalism of litters has been reported in crowded populations of *Mus musculus* (Southwick, 1955) and *Rattus norvegicus* (Boice, 1972).

Definitions of cannibalism vary. They may encompass all intraspecific necrophagy or include only direct killing and subsequent ingestion of conspecifics (Armitage et al., 1979). It is easy to separate the two extremes, but not the intermediate cases. For example, how different is stressing a conspecific to death and subsequently ingesting it from directly killing it and ingesting it? Fox (1975) defined cannibalism as "intraspecific predation" and presented a convincing argument for its potential as a population regulator. He noted that it may occur when vulnerable individuals are present, regardless of food levels or population density. Advantages to the survivor of a cannibalistic encounter include energy gain, elimination of a genetic rival, and reduction of population size which further enhances survival (op. cit.; Armitage et al., 1979). In addition, cannibalism of nestlings by an unrelated male would hasten the return of estrus in the female, which would facilitate a genetic contribution by the male. The confined environment of small islands may bring males into contact with nestlings more frequently than on the mainland. Cannibalism may become disadvantageous when a cannibal becomes so aggressive that reproduction is adversely affected; however, it does allow the reduction of population size before an acute resource shortage causes severe physiological stress in a population (Fox, 1975).

Capillaria hepatica

Although direct evidence of cannibalism (= intraspecific predation) is lacking in this study, is the parasitic nematode *Capillaria hepatica* a reliable indirect indicator of cannibalism? Prevalence of *C. hepatica* infections is higher on islands in Barkley Sound than on the adjacent mainland, and among the islands themselves prevalence increases as island size decreases. Tail wounding indices and presumably aggressiveness among male deermice show a similar pattern.

Therefore it is tempting to invoke a causal relationship between tail wounding and prevalence of *C. hepatica* by assuming that increased fighting results in increased levels of cannibalism among the mice.

Freeman and Wright (1960) argued that seasonal patterns in *C. hepatica* infections in Ontario deermice were likely caused by increased cannibalism during late winter due to increased local densities (communal nesting) and decreased food supplies, but their interpretation of cannibalism is unclear. It is conceivable that the mid-summer low in infection in young deermice from the present study represents a period of minimal environmental stress in which food is abundant, temperatures are mild, and cannibalism occurs relatively infrequently; and therefore release of *C. hepatica* ova is relatively low. Differences in the duration and onset of reproductive activity in mice from different locations likely reflect differences in environmental conditions among locations, and undoubtedly result in different seasonal patterns of aggressiveness in mice among locations (Healey, 1967). The fact that all locations exhibited a similar seasonal pattern of *C. hepatica* infection despite these differences suggests that seasonality is not directly related to changes in aggressiveness. However, the seasonal pattern of mortality due to aggression may differ considerably from the seasonal pattern of aggressiveness itself.

Do predators play an important role in the transmission of *C. hepatica* on either the islands or the mainland? Freeman and Wright (1960) argued that if carnivores are essential to the transmission of *C. hepatica* then the prevalence of metacestode infections in deermice should exceed the prevalence of *C. hepatica* infections. If this argument is valid, the low prevalence of metacestode infections (relative to *C. hepatica* infections) in deermice in this study suggests that carnivores are not essential transmitters, although they may be important on some islands. However, in areas where parasite distributions are patchy, as on islands, this argument may not hold (Holmes, pers. comm.).

Do scavenging beetles act as transmitters of *C. hepatica* in these populations? The role that scavengers play in the dissemination of *C. hepatica* is generally unknown. Momma (1930) considered flies to be important and Mobedi and Arfaa (1971) showed that ground beetles (Carabidae: *Carabus* and *Calatus* spp.) were capable of transmitting embryonated ova. Of the two commonest species in this study only *P. lama* is capable of passing embryonated ova. If *P. lama* is an important disseminator, one would expect higher levels of *C. hepatica* infection on Fleming Island, where *P. lama* is dominant, than on Diana Island, where *S. angusticollis* is dominant. Since the two islands are otherwise comparable (similar mouse densities, shrew densities, and wounding indices) the similarity in prevalence and severity of *C. hepatica* infections between the two islands suggests that *P. lama* is not an important disseminator.

In fact the mouse-beetle interaction experiments strongly suggest that both species of beetles may act as effective interference competitors with deermice for mouse carcasses. Therefore, on the mainland the presence of shrews, quadrupedal predators, and relatively high beetle densities may minimize the number of carcasses available to mice; on Diana and Fleming Islands the presence of shrews, but the relatively low beetle densities and the absence of quadrupedal predators may result in increased numbers of carcasses available; while on Helby Island the relatively low beetle densities in combination with the absence of both shrews and quadrupedal predators likely maximizes the availability of carcasses to mice.

It is likely premature to apply a similar explanation to the pattern of infection among islands in Table 23.

There is an apparent weak inverse relationship between the presence of shrews and the prevalence of *C. hepatica* infections in these islands, but it may be spurious. Relative density estimates of shrews on these islands are unavailable. There are islands that support shrew populations but have high prevalences of *C. hepatica*. More extensive sampling of beetles in space and time would also be useful.

After *C. hepatica* becomes established in an insular mouse population, an infected mouse will likely not disperse from or be removed by a predator from that population. This may help to insure the continued survival of *C. hepatica* and may also help to explain its high prevalence in mice on small islands.

Although cannibalism (= intraspecific predation) undoubtedly occurs in deermouse populations from the Barkley Sound area, especially on the smaller islands, it appears that *C. hepatica* is of limited use as an indicator of it. Freeman and Wright (1960) and Farhang-Azad (1977a,b) considered cannibalism to be the most important egg-disseminating mechanism in their study populations, but neither attempted to discriminate between intraspecific predation and intraspecific necrophagy. Layne (1968) and others (Momma, 1930; Mobedi and Arfaa, 1979) have implicated invertebrate species as disseminators, but the role of competition in the distribution of *C. hepatica* has largely been ignored. In effect, the host, living or dead, represents a food resource for which predators and/or scavengers may compete. Competition among scavengers for mouse carcasses and the distribution of predators, rather than cannibalism, may best account for the distribution and abundance of *C.hepatica* in deermouse populations of the Barkley Sound region. The high prevalence on islands may simply indicate that there is much necrophagy by deermice due to the increased availability of mouse carcasses.

However, the high prevalence of *C. hepatica* in these insular populations does raise several interesting questions:

1. Does the worm itself affect the dynamics of the population, and if so how?

2. Does the increased availability of carcasses significantly affect the resource base of the mouse?

Acute infections are likely more serious than chronic ones. Both *Mus* and *Rattus* show a partial age resistance to the worm (Luttermoser, 1938); therefore acute infections may cause higher mortality in young mice than old. Because of the four-week developmental period between initial infection with *C. hepatica* and the appearance of debilitating symptoms in acutely infected mice (Luttermoser, 1938), mice that acquire acute infections while still in the nest would probably experience greatest mortality when entering subadulthood. The significantly heavier mortality among sub-adults on Helby Island than on Diana and Fleming Islands, or the adjacent mainland, is interesting in this regard. Although regeneration of liver tissue following a severe infection must increase the energy budget of an animal, in all mice examined there was no evidence of poor condition in heavily infected individuals, and all heavily infected adults encountered during the breeding season were fully reproductively active. However, no attempt was made to distinguish between chronic and acute infections. The amount of damage in heavily infected livers suggested that these mice may have less ability to deal with toxic foods than uninfected mice (J. Johnson, pers. comm.), although toxicity related mortality would be hard to observe in the field.

Duration of breeding in deermice is undoubtedly affected to some extent by food availability. Although the correlation may be spurious, among the locations studied seasonally, the Helby Island population, which experienced the least competition for mouse carcasses, was reproductively active for the longest period.

Body Size

Explanation of body size differences between mainland and island populations, and among the island populations themselves is difficult. Although increased size is commonly reported in insular small mammals, I am unaware of any adequate explanation of this pattern. The most difficult aspect of the pattern to accommodate is variability among islands of similar sizes (Foster, 1965; Carlquist, 1974; Redfield, 1976). In Barkley Sound body size appears to increase as island size decreases, but there are exceptions.

It is tempting to invoke a relationship between aggressiveness and body size, although Halpin and Sullivan's (1978) large Gulf Island deermice were clearly non-aggressive. In addition, weights of males and females in Barkley Sound generally did not differ on a given island, which may imply that selective pressures that determine body size are operating in the same way on males and females. Genetic drift may also play an important role, especially on small islands.

Single factor explanations involving isolation, decreased predation, or decreased interspecific competition are likely too simplistic. Several recent studies (Heaney, 1978; Case, 1978) have taken a comprehensive multi-factor approach to this problem.

Heaney (1978) considered predation, food limitation, interspecific competition and selection for physiological efficiency, all of which potentially affect resource availability, to be the major factors that determine body size in mammals. He suggested that these factors are closely interrelated and vary with island size.

Case (1978) used "optimum body size" models, which optimize the net energy gained by an organism, to explain body size changes in insular mammals and reptiles. He predicted that evolutionary increases in body size should occur in populations that experience increased energy supply:energy demand ratios. From his model, one would expect higher equilibrium resource levels in populations of large individuals of a species than in populations of small individuals of the same species. Despite relatively uniform vegetational structure and composition, resource levels in Barkley Sound could vary, but they would be difficult to measure.

Increased body length/tail length ratios are characteristic of *Peromyscus* sp. populations on small, isolated islands (Foster, 1965). The fact that not all large races have short tails indicates that the relative decrease in tail length of island forms is not simply an example of allometric growth (op. cit.). Foster (1965) also documented a decrease in body length/tail length ratio in an insular deermouse population following the introduction of rats to the island.

Kramer (1951) suggested that reduction of limbs and tails in insular lizards may be due to decreased selection for agility in the absence of predators.

In mice, the tail serves both as a balancing and heat regulating organ. In the present study, it is unlikely that temperature regimes differ sufficiently between the islands and the mainland to account for the differences in tail length observed. Do decreased tail lengths on the islands simply reflect reduced agility requirements in the absence of ground predators? Relative tail lengths were consistently smaller in island than in mainland populations, but variation among islands was extensive. Whether this variation is due to different selective regimes or to random genetic processes is unknown.

Rapid growth has been reported in Gulf Island deermice (Sullivan, 1977), but evidence of rapid growth on islands in the present study should be interpreted cautiously. Determination of growth rates from age-weight relationships of dead-trapped mice captured over an entire year is subject to several sources of error. In addition to possible differential survival of individuals that differ in weight, growth of individuals may be affected by season and reproductive condition. On the live-trapping transects, mice grew slowly during the non-breeding season at all locations. However, the length of that season varied among locations. Since the pattern of juvenile recruitment also differed among locations, higher growth rates in young animals on some islands may only reflect earlier juvenile recruitment and/or longer breeding seasons.

These variables, in combination with the allometric effects of attaining ultimately different sizes at different locations, make interpretation of growth rates extremely difficult. A comparison among locations of weight changes in mice first captured as young juveniles during early or mid-breeding season on live-trapping transects would be instructive. However, too few juveniles recruited to mainland populations at that time and too few island juveniles remained on the transects long enough to make a comparison.

Measurements of growth and maturation rates of mainland and island mice under carefully controlled laboratory conditions might provide additional insight in this area.

Theoretical Considerations

Most predictions in the present study can be viewed in the light of r-K selection theory, as outlined by Stearns (1976). Many insular rodent populations apparently tend toward K-selection (Fullaghar et al., 1963; Jewell, 1966; Clough, 1969; Delany, 1970; Redfield, 1976; Tamarin, 1977a,b,c,d).

Barkley Sound populations of *Peromyscus maniculatus* conform to some but not all correlates of K-selection. Population size appears relatively constant, juvenile mortality appears more uncertain than adult mortality, body size is relatively large, and litter size is relatively small. Age distributions of island males are generally top-heavy, but overall survival may actually be lower on some islands than on the mainland. On the other hand, age distributions and overall survival of females differ little between island and mainland populations, and I could not demonstrate higher densities, delayed maturity, or reduced reproductive rates (duration and intensity), all correlates of K-selection, in these island populations.

Reproductive strategies in *P. maniculatus* appear to be temporally dynamic, especially on islands. Varying reproductive efforts make comparison of populations according to r-K criteria difficult (Nichols et al., 1976).

Wilbur et al. (1974) criticized the indiscriminant application of r-K selection theory to account for life history parameters, and warned that its use could obscure the causal factors responsible for the evolution of those parameters. This criticism seems especially appropriate if the carrying capacity or the mechanism of population regulation of a population is unknown. They (op. cit.) also stressed the need for considering as many environmental dimensions as possible. It is obviously dangerous to ignore dimensions of an animal's environment for the sake of simplicity, or to order dimensions subjectively in quest of generalities.

Stearns (1976) suggested that various causal systems may operate simultaneously, with different outcomes for different life history parameters. He (op. cit.) also made several points that may be appropriate to this study: 1) natural selection favours the best of available traits, and not necessarily the optimal trait; 2) in broadly-based field studies there is a danger of giving evolutionary explanations of phenomena without eliminating the non-evolutionary possibilities.

Since deermouse populations in Barkley Sound are likely persistent, especially on islands larger than 25 ha, one would expect some aspects of the animal's biology to reflect this ability to persist. Population densities were not consistently higher on islands than on the mainland, but there was some indication that island populations fluctuated less than mainland ones, despite fluctuating reproductive effort on islands. The relative constancy of population size on islands likely resulted from dispersed juvenile recruitment and fluctuating pre-weaning and early post-weaning mortality. Much of this mortality was probably directly or indirectly effected intraspecifically. Persistence of a population in an environment lacking a dispersal "sink" requires intraspecific control of surplus animals. Rather than decreasing reproductive effort and thus minimizing production of surplus animals, Barkley Sound deermice may be avoiding overpopulation by eating the surplus.

Clearly there were some differences among islands in densities, overall reproductive effort, recruitment patterns, and mortality schedules. Aggressiveness and wounding levels in males and average age of males appeared to increase with decreasing island size, but other parameters showed no definite correlations with island size.

The size of an island is only one of many dimensions of a deermouse's environment. Island environments of deermice in Barkley Sound may differ from one another in other ways, some of which are related to island size and some of which are not. As evidenced from the distribution patterns of *Capillaria hepatica,* trophic relationships of deermice may differ among islands as well as between islands and adjacent mainland. If there is local environmental variation in Barkley Sound, variability in life history parameters among islands may evolve because of a release from the gene flow that likely inhibits local adaptive responses in mainland populations (Foster, 1965; Soulé, 1966).

Alternatively, populations on different islands may be exhibiting multiple strategies in very similar environments or the same strategy at different points in evolutionary time.

Whether due to different selective regimes or to random genetic processes, variation among insular rodent populations is widespread (Delany, 1970; Foster, 1965; Redfield, 1976; Sullivan, 1977).

It is also possible that the size range of islands in the present study was too small to detect some size-related patterns. Comparisons of my data on Barkley Sound deermice with those of Redfield (1976), Sullivan (1977), and Halpin and Sullivan (1978) on Gulf Island deermice reveal some similarities in reproductive and recruitment patterns and in age structures, but some striking differences in levels of abundance and aggressiveness. Some of these differences may reflect differences in island size, since most Barkley Sound islands sampled were relatively small in comparison to Gulf Islands sampled.

Redfield (1976) argued that island populations maintaining high densities with little fluctuation would have little need for a high intrinsic rate of increase and therefore would be less resilient than mainland populations. Sullivan's (1977) results from removal experiments in the Gulf Islands support this idea. However, on islands smaller than those studied by Sullivan environments may be subject to occasional disruption and disaster (e.g. seed crop failure, flooding). Disturbance experiments on the smallest islands supporting deermouse populations might prove instructive.

The pattern of excess production and subsequent removal (probably through cannibalism) that was observed in Barkley Sound deermouse populations possibly reflects a type of "bet-hedging" (Schaffer, 1974), which, although more energetically expensive than simply reducing reproductive effort, may better prepare the population for coping with an unpredictable disturbance.

The increased allotment of energy to non-productive pursuits may help to regulate populations below their carrying capacities (Lidicker, 1962, 1975). The role that aggression plays in population processes of insular *Peromyscus maniculatus* certainly merits further study. If intraspecific aggressiveness is important in stimulating emigration and emigration is frustrated, as on small islands, increased mortality from fighting or from "shock" (Sadleir, 1965) may result. Halpin and Sullivan (1978) have argued that there is no selective advantage to being aggressive unless that aggression results in access to a limited resource (e.g. food, space, water, mates, nesting sites). Studies of resource availability and its relationship with behaviour in insular deermouse populations would be useful.

In summary, mainland and island populations differed in many respects. Although densities were not consistently different, variance of population size through time appeared lower on some islands than on the mainland. Reproductive activity was similar on islands and mainland in 1977, but breeding in 1976 was prolonged on islands. Island litters were consistently smaller than mainland litters, but there was little evidence of overall reduction in reproductive effort on islands. Juvenile recruitment was generally more dispersed throughout the breeding season on islands than on the mainland. Island males were generally more aggressive than mainland males. Survival of juvenile recruits (particularly males) to sub-adulthood was lower on some but not all islands than on the mainland. In comparison to the mainland, age distributions of males on most islands were top-heavy. Body weights and body length/tail length ratios of island mice consistently exceeded those of mainland mice. Based on infection levels of *Capillaria hepatica*, ingestion of mouse carcasses by mice was more common in island than in mainland populations.

Variation in densities, overall reproductive effort, recruitment patterns, and mortality schedules was apparent among islands, but did not correlate clearly with island size. On the other hand, aggressiveness and wounding levels in males and average age of males generally increased with decreasing island size.

Differences in amplitude of density oscillations, size of litters, pattern of juvenile recruitment, age structure, and morphological attributes that were observed between populations in the present study are generally compatible with theoretical predictions made by island biologists to date. However, the lack of consistent density differences between islands and mainland, and the increased aggressiveness observed in island populations suggest that some theoretical predictions of island biology should be reappraised.

It is difficult to separate evolutionary and environmental components in the differences observed between mainland and island populations. To do so convincingly requires carefully controlled laboratory measurements of heritability of those traits that were observed in the field. However, the introduction experiments conducted in the Ross Islets provide a first approximation, and strongly suggest that both evolutionary and environmental components are present and can be separated to a limited extent.

Table 1. Some correlates of r- and K-selection (taken from Stearns, 1976).

	r-selection	K-selection
Climate	variable and/or unpredictable	constant and/or predictable
Population size	variable in time non-equilibrium usually below carrying capacity frequent recolonization necessary	constant in time equilibrium near carrying capacity no recolonization necessary
Mortality	density-independent uncertain adult survival	density-dependent uncertain juvenile survival
Survivorship	often Type III (Deevey, 1947)	usually Types I and II (Deevey, 1947)
Selection favours	high r-max early reproduction high resource thresholds small body size semelparity increased birth rate	competitive ability delayed reproduction low resource thresholds large body size iteroparity decreased death rate
Length of life	short	long
Leads to	productivity	efficiency
Proportion of energy allocated to reproduction	relatively large	relatively small
1. Mass offspring/ parent/brood	larger	smaller
2. Mass offspring/ parent/lifetime	larger	smaller

Table 2. Comparison of monthly live-trap captures (from February 1976 to October 1977) among locations by Kruskal-Wallis analysis of variance; values from Figure 2.

Sex	Age	Average rank[1]					H statistic[2]	Multiple pairwise comparisons of confidence intervals[3]
		HA	HB	DI	M1	M2		
Male	Adult	56.5	19.2	52.2	61.3	75.8	39.52***	HB DI HA M1 M2
	All	49.9	15.7	62.7	65.7	71.0	44.98***	HB HA DI M1 M2
Female	Adult	41.0	22.0	67.4	56.7	77.9	44.29***	HB HA M1 DI M2
	All	36.0	20.0	69.9	64.6	74.5	51.38***	HB HA M1 DI M2

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[1] HA = Haines Is., HB = Helby Is., DI = Diana Is., M1 = Mainland 1, M2 = Mainland 2

[2] H adjusted for ties according to Marascuilo and McSweeney (1977)

[3] locations underlined do not differ significantly ($p > 0.05$)

*** $p < 0.001$

Table 3. Values from χ^2 test for heterogeneity in catch per unit effort among the monthly dead-trap samples shown in Figure 3.

Location	χ^2
Helby Island	20.02*
Diana Island	60.77***
Fleming Island	38.44***
Mainland	102.39***

*,*** $p < 0.05$, < 0.001

Table 4. A comparison of catch per unit effort between locations; combined totals for both sexes from monthly dead-trap transects for all months.

Location	Catch	Effort (no. trap nights)
Helby Island	194	1385
Diana Island	229	1633
Fleming Island	232	1697.5
Mainland	493	3915

$\chi^2_{\text{among locations}^*} = 3.10$

[*] calculated from catch and effort minus catch

Table 5. Effects of "edge" on catch per unit effort in monthly dead-trap samples (see text for details).

Location	Σ Catch/no. of adjusted trap nights Decad of trap points					t value from paired comparisons[1]		
	1	2	3	4	5	1 vs.2	1 vs.5	2 vs.5
Helby Is.	91/316	58/347.5	46/365.5	57/361.5	50/359.5	3.08**	2.89**	0.95
Diana Is.	97/411.5	64/420	59/425	51/414	68/420	2.76**	2.11*	0.37
Fleming Is.	71/412	58/429.5	58/436	57/431	63/424.5	1.36	0.80	0.56
Mainland	150/935.5	105/974.5	116/983.5	110/986	131/974	2.12*	2.97**	0.40

[1] significance levels are for 1-tailed test

*,** $p < 0.05$, < 0.01

Table 6. Mean number ($\overline{x}$) and variance (s^2) of monthly live-trap captures (for 21 months at each location), and F_{max}-test for homogeneity of variance among locations.

Sex	Age		Location					F_{max}-test
			Haines	Helby	Diana	Mainland 1	Mainland 2	s^2_{max}/s^2_{min}
Males	Adult	$\overline{x}$	16.43	8.43	15.19	17.57	19.10	
		s^2	17.26	6.46	28.46	63.16	46.49	9.78**
	All ages	$\overline{x}$	19.52	10.43	21.62	23.24	24.90	
		s^2	20.76	16.46	35.25	41.22	58.83	3.54*
Females	Adult	$\overline{x}$	10.52	7.71	14.76	13.05	17.62	
		s^2	8.66	3.61	17.49	23.55	36.05	9.99**
	All ages	$\overline{x}$	13.14	10.05	20.95	19.43	22.57	
		s^2	14.33	4.65	19.45	43.96	56.06	12.06**

*,** $p < 0.05$, < 0.01

Table 7. Litter size in deermice from monthly dead-trap transects: nested analysis of variance (locations nested by months); multiple comparison among means; and analysis of variance for seasonal variation (by combining monthly samples in three groups: April-July, August-October, November-March) within locations.

		Location			
		Helby	Diana	Fleming	Mainland
$\bar{x}$ litter size		3.95	3.61	3.72	4.42
n		77	85	60	113
Nested anova					
locations			F = 13.50***		
months			0.92		
Multiple comparisons among means[1]			MLD $\underline{\text{H F D}}$*,**		
Anova for seasonal variation within locations	F =	0.24	0.33	1.19	1.37

[1] tested by "Student-Newman-Keuls" test (Sokal and Rohlf, 1969). Locations underlined do not differ significantly.

*,**,*** $p < 0.05$, < 0.01, < 0.001

Table 8. Mean number ($\bar{x}$) and mean rank ($\bar{R}$) of social interactions per encounter in arena experiments.

Behaviour		Mainland			Diana	Helby	Haines
		1	2	1 + 2			
Approach	$\bar{x}$	4.3	3.7	4.0	4.5	5.6	4.3
	$\bar{R}$	24.1	19.3	21.7	26.0	32.7	25.5
Investigatory	$\bar{x}$	1.2	2.4	1.8	3.5	2.4	3.5
	$\bar{R}$	15.3	23.6	19.4	30.3	25.0	33.4
Cohesive	$\bar{x}$	0	0.4	0.2	0.7	0	0
	$\bar{R}$	22.5	27.6	25.0	32.5	22.5	22.5
Agonistic (Σ)	$\bar{x}$	8.8	8.0	8.4	8.6	12.6	14.0
	$\bar{R}$	23.1	19.2	21.2	20.3	31.4	33.7
Aggressive	$\bar{x}$	1.4	0.3	0.9	0.8	2.5	3.9
	$\bar{R}$	26.6	15.2	20.9	18.6	26.8	40.2
Defensive	$\bar{x}$	7.4	7.7	7.6	7.8	10.1	10.1
	$\bar{R}$	25.3	19.3	22.3	22.4	31.5	29.1
All interactions	$\bar{x}$	14.3	14.5	14.4	17.3	20.6	21.8
	$\bar{R}$	21.0	19.8	20.4	23.6	30.9	32.3

Table 9. Kruskal-Wallis analysis of variance among locations (with mainland samples separate and combined) in social interactions in arena experiments.

Behaviour	H[1] (M1, M2, DI, HB, HA)	H[1] (M1+2, DI, HB, HA)	Comparisons among means[2]
Approach	4.45	3.88	
Investigatory	9.43	7.74	
Cohesive	11.76*	10.25*	HA HB M1 M2 DI HA HB M1+2 DI
Agonistic (Σ)	8.28	7.91*	
Aggressive	18.84***	15.52***	M2 DI M1 HB HA
Defensive	4.57	3.71	DI M1+2 HB HA
All interactions	6.30	6.27	

[1] H values corrected for ties according to Marascuilo and McSweeney (1977).

[2] Locations underlined do not differ significantly ($p > 0.05$); from multiple confidence intervals procedure for Kruskal-Wallis ANOVA (Marascuilo and McSweeney, 1977).

*,*** $p < 0.05$, < 0.005

Table 10. Tail wounding in adult deermice from monthly live-trap samples, combined into non-breeding season (NB) and 1976 and 1977 breeding seasons (B_1,B_2).

Sex	Tail wound index[1]	Location (no. of mice)														
		Haines Island			Helby Island			Diana Island			Mainland 1			Mainland 2		
		B_1	B_2	NB	B_1	B_2	NB	B_1	B_2	NB	B_1	B_2	NB	B_1	B_2	NB
Males	N	53	16	6	22	17	8	58	47	9	65	79	61	55	67	76
	L	59	36	23	23	29	7	49	77	13	28	72	21	36	76	46
	M	48	47	6	30	15	3	25	31	2	11	18	10	7	33	9
	S	23	13	4	17	2	1	9	1	0	0	3	0	4	6	3
Females	N	60	35	17	72	29	--	130	122	19	68	87	51	132	64	52
	L	9	43	13	12	23	--	14	15	5	6	36	11	20	72	21
	M	10	24	5	5	18	--	0	0	0	0	7	2	1	4	3
	S	1	0	0	0	2	--	0	0	0	0	0	0	0	0	0

[1] N = nil, L = light, M = moderate, S = severe

Table 11. Summary of comparisons of wounding levels on live-trap transects, within and among locations, from Table 10.

Location	Males		Females	
	B_1,B_2 vs. NB	B_1 vs. B_2	B_1,B_2 vs. NB	B_1 vs. B_2
Haines Island (HA)	$B_1 > NB^*$ $B_2 > NB^{**}$	$B_1 < B_2^{**}$	$B_1 < NB^{**}$ $B_2 \simeq NB$	$B_1 < B_2^{***}$
Helby Island (HB)	$B_1,B_2 \simeq NB$	$B_1 > B_2^{***}$	--	$B_1 < B_2^{***}$
Diana Island (DI)	$B_1,B_2 \simeq NB$	$B_1 < B_2^{***}$	$B_1 < NB^*$ $B_2 \simeq NB$	$B_1 \simeq B_2$
Mainland 1 (M1)	$B_1 \simeq NB$ $B_2 > NB^{**}$	$B_1 < B_2^*$	$B_1,B_2 \simeq NB$	$B_1 < B_2^{***}$
Mainland 2 (M2)	$B_1 \simeq NB$ $B_2 > NB^{***}$	$B_1 < B_2^{**}$	$B_1 < NB^{***}$ $B_2 > NB^{***}$	$B_1 < B_2^{***}$
Pairwise comparisons among locations[1] (p < 0.005)	B_1	M1 M2 DI HA HB		M1 DI M2 HB HA
	B_2	M1 M2 DI HB HA		DI M1 M2 HB HA
	NB	M1 M2 DI HB HA		M2 M1 DI HB HA

[1] Locations underlined do not differ significantly. Individual pairwise contrasts are considered significant at 0.005 to avoid increased TYPE I error (α = 0.05/ total no. possible pairwise combinations)

*,**,*** $p < 0.05$, < 0.01, < 0.005

Table 12. Tail wounding in young (juvenile and sub-adult) deermice from monthly live-trap samples; all monthly samples combined.

Sex	Tail wound index*	Location				
		Haines Island	Helby Island	Diana Island	Mainland	
					1	2
Males	N	47	36	124	117	94
	L	15	6	6	7	5
	M	1	0	2	0	0
	S	3	0	0	0	0
Females	N	56	45	126	126	98
	L	1	4	4	10	7
	M	0	0	0	0	0
	S	0	0	0	0	0

*N = nil, L = light, M = moderate, S = severe

Table 13. Tail wounding in adult and young (juvenile, sub-adult) deermice from dead-trap samples; A - totals from 11 monthly samples (Mar. 1976 - Jan. 1977); B - totals from 22 islands and the adjacent mainland (mid-May - late June 1977).

Sex	Tail wound index[1]	Location no. mice adults (young)					
		A[2,3]				B	
		H	D	F	Mld	Σ Islands	Mld
Males	N	25 (13)	43 (28)	48 (26)	174 (37)	43	32
	L	54 (1)	60 (0)	64 (1)	69 (3)	85	37
	M	11 (1)	24 (0)	14 (0)	11 (0)	34	5
	S	37 (0)	19 (0)	15 (0)	3 (0)	9	1
		H = 127.0***	Mld F D H			χ^2 = 14.10**	
Females	N	73 (28)	82 (11)	85 (17)	159 (47)	84	16
	L	23 (1)	24 (0)	27 (0)	25 (3)	60	14
	M	4 (0)	6 (0)	3 (2)	1 (0)	10	2
	S	2 (0)	2 (0)	1 (0)	0 (0)	0	3
		H = 12.97**	Mld F D H			χ^2 = 0.45	

[1] N = nil, L = light, M = moderate, S = severe

[2] H = Helby Island, D = Diana Island, F = Fleming Island, Mld = mainland

[3] analyzed by Kruskal-Wallis ANOVA. Locations underlined are not significantly different ($p > 0.05$); from multiple confidence intervals procedure (Marascuilo and McSweeney, 1977).

,* $p < 0.01$, < 0.001

Table 14. Tail wounding in adult deermice from mainland and Helby Island populations introduced to the Ross Islets; all monthly samples at each location combined.

Sex	Tail wound index[1]	Mainland	Helby Island
Males	N	32	19
	L	35	35
	M	9	14
	S	0	4
		$\chi^2 = 9.88^{**}$ (with M,S combined $\chi^2 = 6.30^{*}$)	
Females	N	43	46
	L	17	42
	M,S	11	6
		$\chi^2 = 9.31^{***}$	

[1] N = nil, L = light, M = moderate, S = severe

*,**,*** $p < 0.05, < 0.025, < 0.01$

Table 15. Mean ranks of length of life on live-trapping transects, according to age at first capture; summary of comparisons among locations by Kruskal-Wallis analysis of variance for animals first captured between January 1976 and May 1977. Data from Figure 5.

Age at first capture	Sex		Location[1] (mean rank/number of mice)					H^2
			HA	HB	DI	M1	M2	
Adult	Male	$\overline{R}$	104.9	104.9	102.8	112.4	111.6	0.87
		n	53	28	31	49	54	
	Female	$\overline{R}$	56.1	64.4	59.7	63.4	64.8	1.05
		n	22	15	22	26	38	
Juvenile-sub-adult	Male	$\overline{R}$	51.1	35.9	63.3	71.2	80.4	18.66***
		n	14	18	40	30	23	
	Female	$\overline{R}$	64.1	54.1	80.0	81.9	69.6	7.02
		n	22	20	36	32	33	

[1] HA = Haines Island, HB = Helby Island, DI = Diana Island, M1 = Mainland 1, M2 = Mainland 2

[2] H adjusted for ties according to Marascuilo and McSweeney (1977).

*** $p < 0.001$; HB HA DI M1 M2, locations underlined are not significantly ($p > .05$) different.

Table 16. Age distribution of deermice from dead-trap samples according to sex. Age categories based on tooth wear index of Foster (1965).

Sex	Monthly location[2] (no. mice)					Blitz location (no. mice)		
	Age[1]	H	D	F	Mld	Age[1]	Islds.	Mld
Males	1-2	32	37	35	79	2	2	0
	3	47	83	46	113	3	3	7
	4	35	38	40	39	4	67	33
	5-6	20	9	24	36	5	87	30
						6	19	3
		H = 9.24*		Mld D F H[3]			$\chi^2 = 8.75^*$	
Females	1-2	28	21	38	70	2	3	0
	3	45	64	54	85	3	15	4
	4	26	21	22	36	4	70	15
	5-6	15	10	13	27	5	59	11
						6	14	1
		H = 3.55		Mld F D H[3]			$\chi^2 = 1.44$	

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[1] 1-2 - generally juveniles and sub-adults respectively; 3 - adults probably <6 mos, old; 4 - adults, 6-12 mos.; 5-6 - old adults > and >>12 mos.

[2] H = Helby Island, F = Fleming Island, D = Diana Island; Mld = mainland

[3] Kruskal-Wallis ANOVA and summary of multiple pairwise comparisons of confidence intervals (Marascuilo and McSweeney, 1977); groups underlined are not significantly different ($p > 0.05$)

* $p < 0.05$

Table 17. Sex ratios in monthly dead-trap samples; comparisons among locations, and deviation from 1:1 within locations.

Age	Sex	Location[1]				Comparison among locations
		H	D	F	Mld	
1-2	F	28	21	38	70	
	M	32	37	35	79	$\chi^2 = 3.42$
	1:1		*			
3	F	45	64	54	85	
	M	47	83	46	113	$\chi^2 = 3.99$
	1:1				*	
4	F	26	21	22	36	
	M	35	38	40	39	$\chi^2 = 3.08$
	1:1		*	*		
5-6	F	15	10	13	27	
	M	20	9	24	36	$\chi^2 = 1.62$
	1:1					
Σ	F	114	116	127	218	
	M	134	167	145	267	$\chi^2 = 2.19$
	1:1		***		*	

[1] H = Helby Island, D = Diana Island, F = Fleming Island, Mld = mainland

*,*** $p < 0.05$, < 0.005

Table 18. Embryo resorption in deermice from monthly and blitz dead-trap transects.

	Monthly dead-trap transects[1]				Biltz dead-trap transects	
	H	D	F	Mld.	Islds.	Mld.
Σ litters examined	21	23	16	24	86	11
Σ live embryos	98	88	57	94	308	43
Σ dead embryos	1	0	0	6	14	0
Resorption frequency[2]	.01	0	0	.06	.04	0
Mld. vs. Σ Islds. (live/dead)[3]	$\chi^2 = 8.49$**				$\chi^2 = 0.94$	

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[1] H = Helby Island, D = Diana Island, F = Fleming Island, Mld. = mainland

[2] this represents a conservative estimate because litters examined included early and mid-term as well as late-term pregnancies

[3] tested by χ^2 with Yates' correction

** $p < 0.01$

Table 19. Embryo resorption in deermice from dead-trap transects on 22 islands in Barkley Sound; total from 11 islands (<33 ha) compared with total from 11 islands (>45 ha).

	Islands	
	(<33 ha)	(>45 ha)
Σ dead embryos	11	3
Σ live embryos	125	183

$\chi^2_{\text{with Yates' correction}} = 8.19^{**}$

$^{**}p < 0.01$

Table 20. Survival of juveniles to sub-adulthood in populations from monthly dead-trap transects (see text for details).

Pelage	Location[1] (no. mice)				
	H	D	F	Mld	
Juvenile	30	17	18	44	$\chi^2 = 11.34^{**}$
Non-juvenile	30	41	55	105	
Σ age 1-2	60	58	73	149	
% young animals (age 1-2) in juvenile pelage	50.0	29.3	24.7	29.5	

[1] H = Helby Island, D = Diana Island; F = Fleming Island, Mld = mainland

** $p < 0.01$

Table 21. Survival of recruits to introduced populations in the Ross Islets (see text for details).

Sex		Stock		
		Helby	Mainland	
Males	known alive at final rota	10	17	$\chi^2 = 5.23^*$
	not known alive	11	4	
Females	known alive	18	9	$\chi^2 = 0.62$
	not known alive	8	2	
Σ	known alive	28	26	$\chi^2 = 4.14^*$
	not known alive	19	6	

$^*p < 0.05$

Table 22. Prevalence (% infected) and severity of *Capillaria hepatica* infections and prevalence of *Mesocestoides* sp. in deermice from monthly dead-trapping transects; totals from 11 monthly samples for each location (both sexes included). Host age categories based on tooth wear index of Foster (1965).

Host age	Locations												Pairwise multiple comparisons[2] ($p < .05$)
	Mainland			Fleming Island			Diana Island			Helby Island			
		C. hepatica			*C. hepatica*			*C. hepatica*			*C. hepatica*		
	No. mice exam.	% infected	Severity (P,H)[1]	No. mice exam.	% infected	Severity (P,H)	No. mice exam.	% infected	Severity (P,H)	No. mice exam.	% infected	Severity (P,H)	
1-2	148	10.1	(.73,.27)	73	23.3	(1.00,0)	55	20.0	(.82,.18)	59	37.3	(.86,.14)	Mld F D H
3	196	12.1	(.83,.17)	100	47.0	(.85,.15)	141	51.1	(.86,.14)	91	82.4	(.72,.28)	Mld F D H
4	73	26.0	(.95,.05)	61	67.2	(.88,.12)	57	73.7	(.67,.33)	60	85.0	(.47,.53)	Mld F D H
5-6	61	34.4	(.81,.19)	37	86.5	(.56,.44)	18	88.9	(.75,.25)	35	94.3	(.48,.52)	Mld F D H
Σ[3]	482	15.9	(.84,.16)	271	50.6	(.81,.19)	273	51.6	(.79,.21)	246	74.0	(.62,.38)	Mld F D H
Pairwise multiple comparisons[2]	1-2 3 4 5-6			1-2 3 4 5-6			1-2 3 4 5-6			1-2 3 4 5-6			
Mesocestoides sp. prevalence[4] (% infected)	1.2 (1.5)			4.1 (5.5)			0.4 (0.4)			0.8 (1.2)			

[1] P = present (light or moderate), H = heavy

[2] Groups underlined are not significantly different

[3] Includes four animals not aged

[4] Figures outside parentheses represents mice that contained larvae encysted in the liver or free-living in the peritoneal or pleural cavities; figure in parentheses includes mice that lacked larvae but exhibited liver damage characteristic of heavy *Mesocestoides* infections in which larvae were present.

Table 23. Prevalence (% infected) and severity of *C. hepatica* infections and prevalence of *Mesocestoides* sp. in deermice from blitz dead-trapping transects. Age categories (from carcasses with skulls intact) based on tooth wear index of Foster (1965).

Location	Island size (ha)	Total number mice examined	*C. hepatica*			*Mesocestoides* sp. Prevalence[2] (% infected)
			Prevalence (% infected)	Severity[1]		
				P	H	
Fry	5.2	4	100	.75	.25	0 (25)
Keith*	7.3	20	100	.60	.40	40 (40)
Erin	8.2	8	88	.75	.25	0 (25)
Walsh	10.5	3	100	1.00	0.00	0
Austin	13.4	11	100	.82	.18	0 (9)
Mullins	13.7	7	100	.75	.25	29 (29)
Chalk	14.8	5	60	1.00	0.00	0
Bauke	14.8	10	80	.38	.62	0
Prideaux*	25.8	15	93	.86	.14	27 (27)
Sandford	30.8	23	78	.67	.33	0
Cooper	32.7	21	76	.69	.31	0
Willis	45.1	29	59	1.00	0.00	0
Jarvis*	48.9	18	72	.92	.08	28 (33)
Dodd*	84.6	14	71	.90	.10	0
Gibraltar*	85.0	21	76	.94	.06	33 (38)
Edw. King*	93.5	11	82	.89	.11	0 (9)
Turtle*	110.2	13	69	1.00	0.00	0
Nettle*	145.9	30	87	.92	.08	17 (17)
Diana*	174.0	25	68	1.00	0.00	4 (16)
Effingham	232.6	31	90	.89	.11	0
Fleming*	291.4	10	80	1.00	0.00	0
Tzartus*	1683.1	12	83	.80	.20	0 (17)
Σ Islands (all ages)		341	80	.85	.15	9 (13)
Mainland* (all ages)		110	36	.87	.13	0 (3)
Mainland age	2	1	0	0.00	0.00	
	3	11	55	.50	.50	
	4	49	33	.94	.06	
	5	42	38	.94	.06	
	6	4	25	1.00	0.00	
Σ Islands	2	5	0	0.00	0.00	
	3	18	78	.93	.07	
	4	136	74	.91	.09	
	5	146	86	.84	.16	
	6	34	94	.63	.37	

[1] P = present (light or moderate), H = heavy

[2] Figure outside parentheses represents mice that contained larvae encysted in the liver or free-living in the peritoneal or pleural cavities; figure in parentheses includes mice that lacked larvae but exhibited liver damage characteristic of heavy *Mesocestoides* infections in which larvae are present.

* denotes presence of shrews (*Sorex obscurus*) in that location, according to Guiguet (1974)

Table 24. Summary of relative abundances (catch per unit effort) of scavenging insects caught in pitfall traps and of shrews caught in break-back traps from three islands in Barkley Sound and the adjacent mainland (see text for details).

Location	Pitfall captures (no. individuals)[1]						Shrews *Sorex obscurus* (no./trap nights)
	Scaphinotus angusticollis	*Pterostichus lama*	*P. crenicollis*	*P. algidus*	*P. pumilus*	*Zacotus matthewsii*	
Helby Island	11	1					absent
Diana Island	11		1				21/1871
Fleming Island	1	13					21/1847
Mainland 1	76		1			3	
Mainland 2	134		3	8	1		15/4437
	$H^2 = 52.16^{***}$	D H F Mld 1 Mld 2					$\chi^2 = 18.4^{***}$

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[1] same trapping effort (42 trap nights) for each location

[2] from Kruskal-Wallis ANOVA of abundance by location, for the combined catches of the two largest and numerically dominant spp., *S. angusticollis* and *P. lama* from each trap point along a transect. Locations underlined are not significantly different ($p > 0.05$).

*** $p < 0.001$

Table 25. Dominance in three vegetation layers and deadfall indices along the permanent live-trap transects. Dominance quantities refer to the number of 10 m segments, at each location, in which a species was most prevalent and/or second most prevalent by percent cover. See text for details. Nomenclature follows Hitchcock and Cronquist (1973).

Species	Location				
	Haines	Helby	Diana	Mld 1	Mld 2
Canopy					
Tsuga heterophylla	48	49	46	38	45
Thuja plicata	2	0	4	8	0
Picea sitchensis	2	0	2	0	8
Abies amabilis	0	0	0	8	0
Alnus rubra	0	0	0	0	3
Open	8	11	8	6	4
Understory/shrub					
Open	27	25	24	16	39
Gaultheria shallon	10	11	17	19	2
Vaccinium parvifolium	5	9	4	13	4
Vaccinium ovatum	9	10	13	1	0
Tsuga heterophylla	1	5	1	6	4
Menziesia ferruginea	1	0	1	1	5
Rubus spectabilis	6	0	0	1	3
Vaccinium alaskaense	1	0	0	2	3
Abies amabilis	0	0	0	1	0
Herbaceous					
Duff/moss	34	30	37	32	33
Blechnum spicant	22	27	17	28	21
Polystichum munitum	3	0	0	0	4
Vaccinium parvifolium	0	0	3	0	2
Vaccinium ovatum	1	1	2	0	0
Tsuga heterophylla	0	2	1	0	0
Deadfall indices	91	73	69	78	104

Table 26. Summary of maximum-minimum temperatures for approximate four-week periods from 28 November 1976 to 7 October 1977, and total precipitation at three locations. See text for details.

	Helby Island		Bamfield		Mainland 2	
	Max. (°C)	Min. (°C)	Max. (°C)	Min. (°C)	Max. (°C)	Min. (°C)
28 Nov. - 26 Dec.	11.0	4.5	11.5	2.5	11.5	3.0
- 23 Jan.	9.5	1.0	10.5	-1.5	10.0	-1.0
- 20 Feb.	9.5	1.0	8.0	-1.0	9.0	-0.5
- 20 Mar.	7.5	0.5	7.0	-0.5	8.0	-0.5
- 17 Apr.	12.5	2.0	14.0	1.0	13.0	0.5
- 15 May	14.5	3.0	16.0	2.5	14.5	0.5
- 12 June	16.5	5.0	14.0	4.0	14.0	3.0
- 11 July	16.5	9.5	18.5	6.5	18.0	5.5
- 11 Aug.	18.5	9.0	22.5	7.0	19.0	6.0
- 9 Sept.	20.0	10.0	21.5	8.0	20.5	6.5
- 7 Oct.	17.0	7.0	18.5	3.5	17.0	2.0
$\overline{x}$ (max., min.)	13.9	4.8	14.7	2.9	14.1	2.3
Range - max.	+7.5-20.0		+7.0-22.5		+9.0-20.5	
min.	+0.5-10.0		-1.5- 8.0		-1.0- 6.5	
$\overline{x}$ (max.-min.)	9.2		10.9		11.8	
Range	7.0-11.5		7.5-15.5		8.5-15.0	
Σ precipitation (cm) (1 Dec. 76-7 Oct. 77)	162		179		205	

Figure 1. Map of study area.

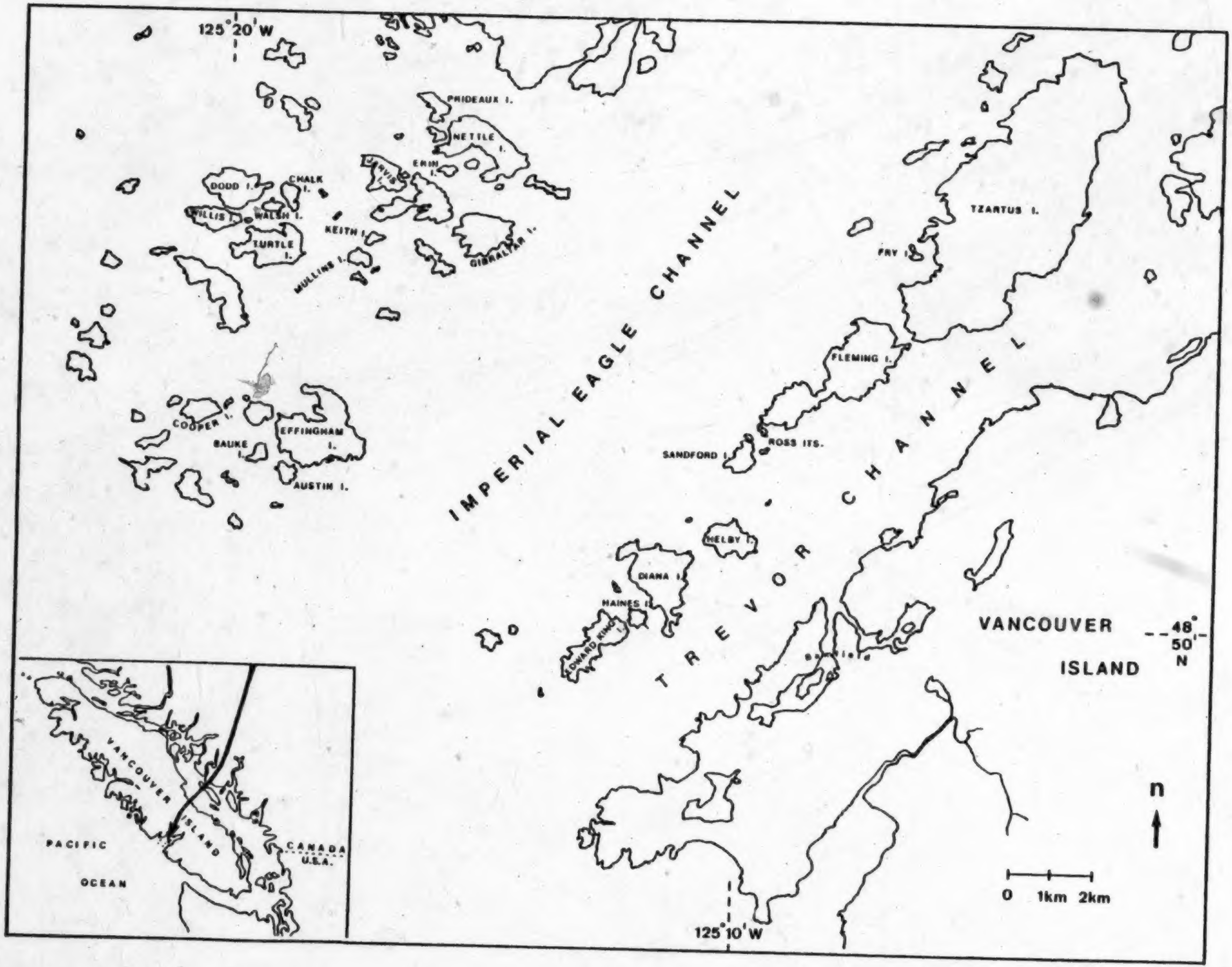
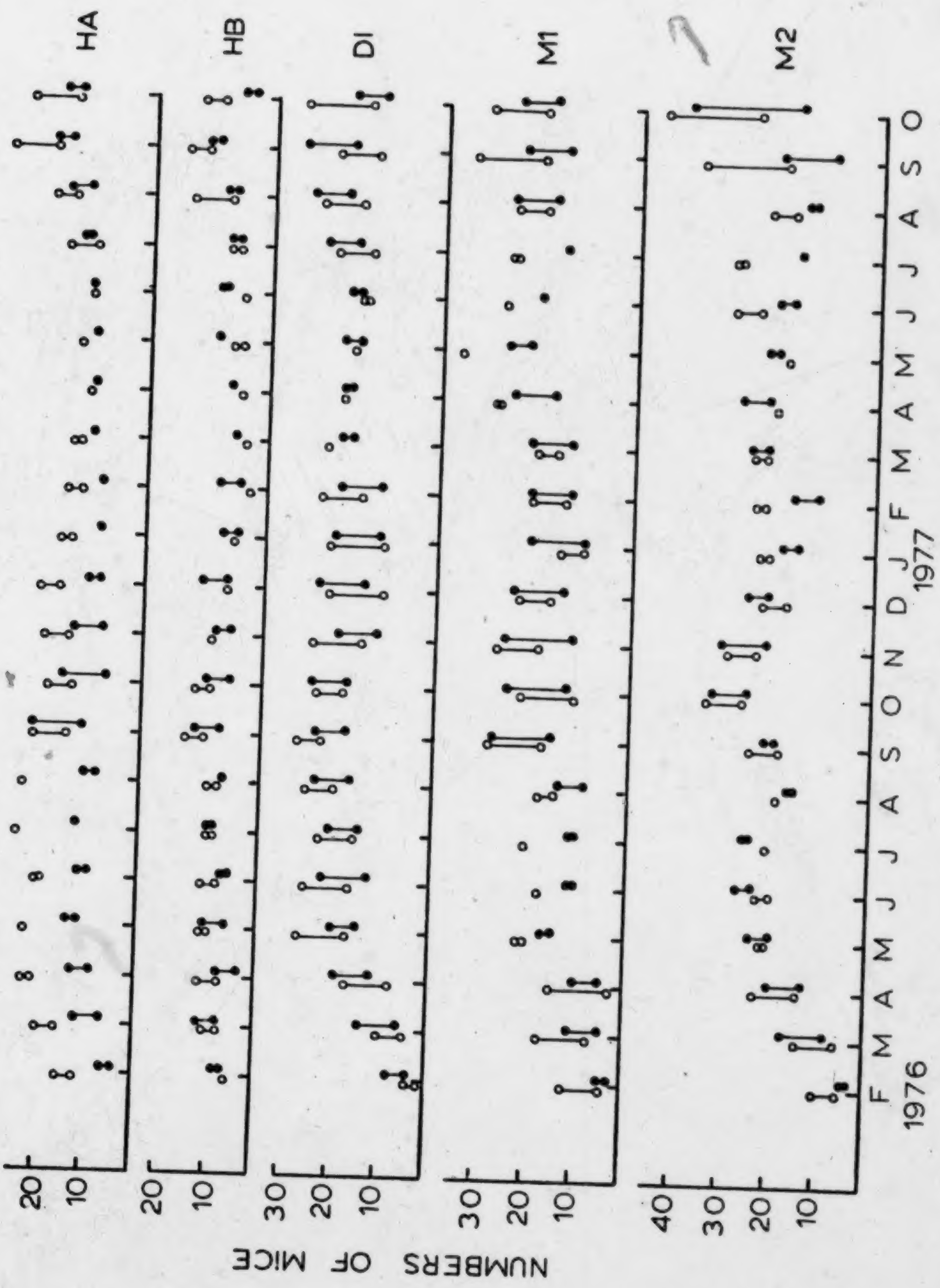

125°20'W
PRIDEAUX I.
NETTLE I.
ERIN I.
JARVIS I.
DODD I.
CHALK I.
WILLIS I.
WALSH I.
TURTLE I.
KEITH I.
MULLINS I.
GIBRALTAR I.
COOPER I.
BAUKE I.
EFFINGHAM I.
AUSTIN I.
IMPERIAL EAGLE CHANNEL
TZARTUS I.
FRY I.
FLEMING I.
ROSS ITS.
SANDFORD I.
HELBY I.
DIANA I.
HAINES I.
EDWARD KING I.
TREVOR CHANNEL
Bamfield
VANCOUVER ISLAND
48°50'N
125°10'W
n
0 1km 2km
VANCOUVER ISLAND
PACIFIC OCEAN
CANADA
U.S.A.

Figure 2. Monthly captures of deermice on live-trapping transects, from February 1976 to October 1977. Data points for total captures (above) and adult captures (below) joined by vertical lines for both sexes in each month. HA = Haines Island, HB = Helby Island, DI = Diana Island, M1 = Mainland 1, M2 = Mainland 2, open circles = males, closed circles = females.


HA
HB
DI
M1
M2
NUMBERS OF MICE
20
10
20
10
30
20
10
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20
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F
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1976
1977

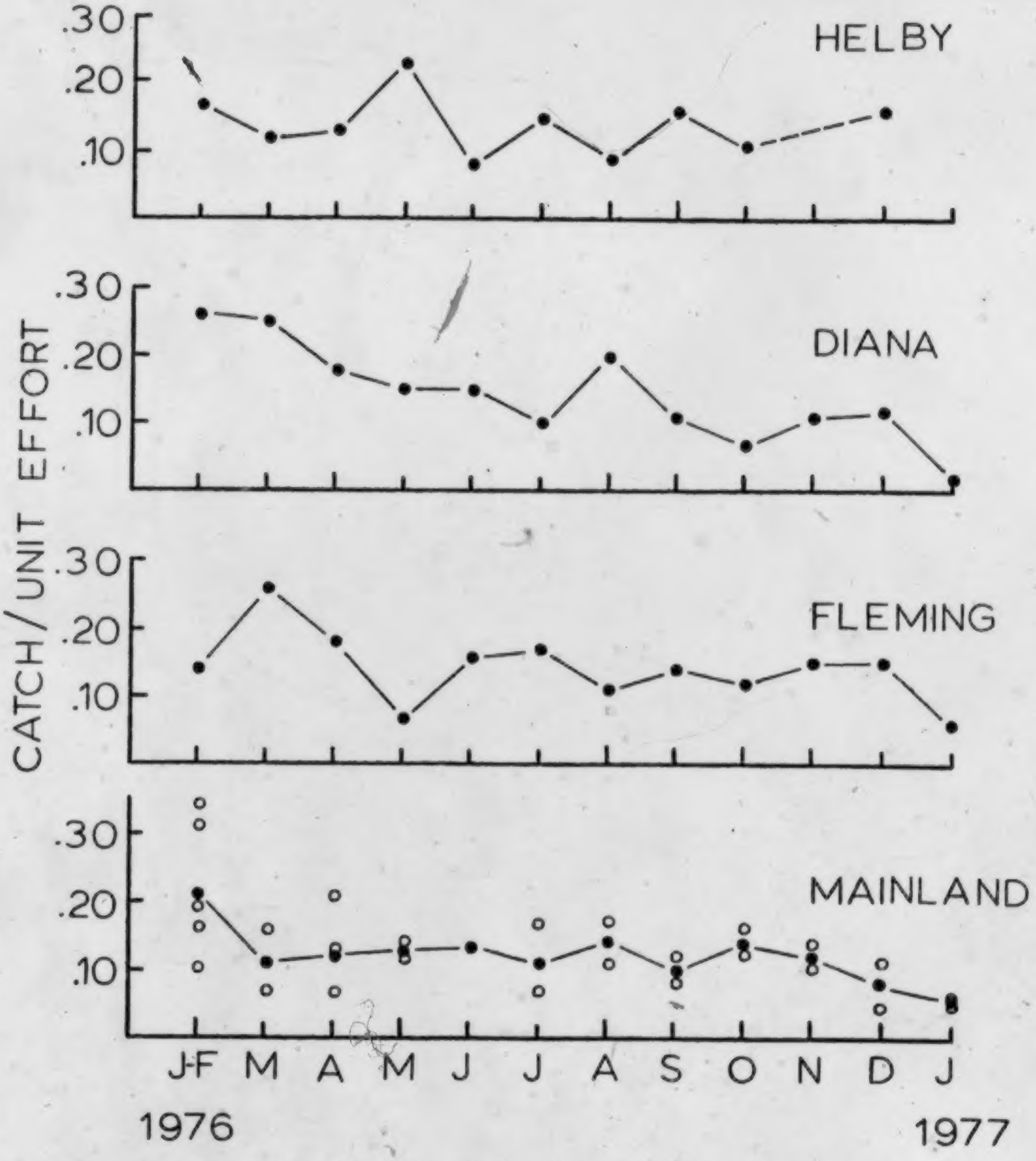


Figure 3. Catch per unit effort in monthly dead-trap transects from Helby, Diana and Fleming Islands, and from the adjacent mainland, from January 1976 to January 1977. Data from first 10 trap points at each location excluded due to edge effect (see text for details). Open circles in mainland data represent individual sites, closed circles represent all sites combined for each month.

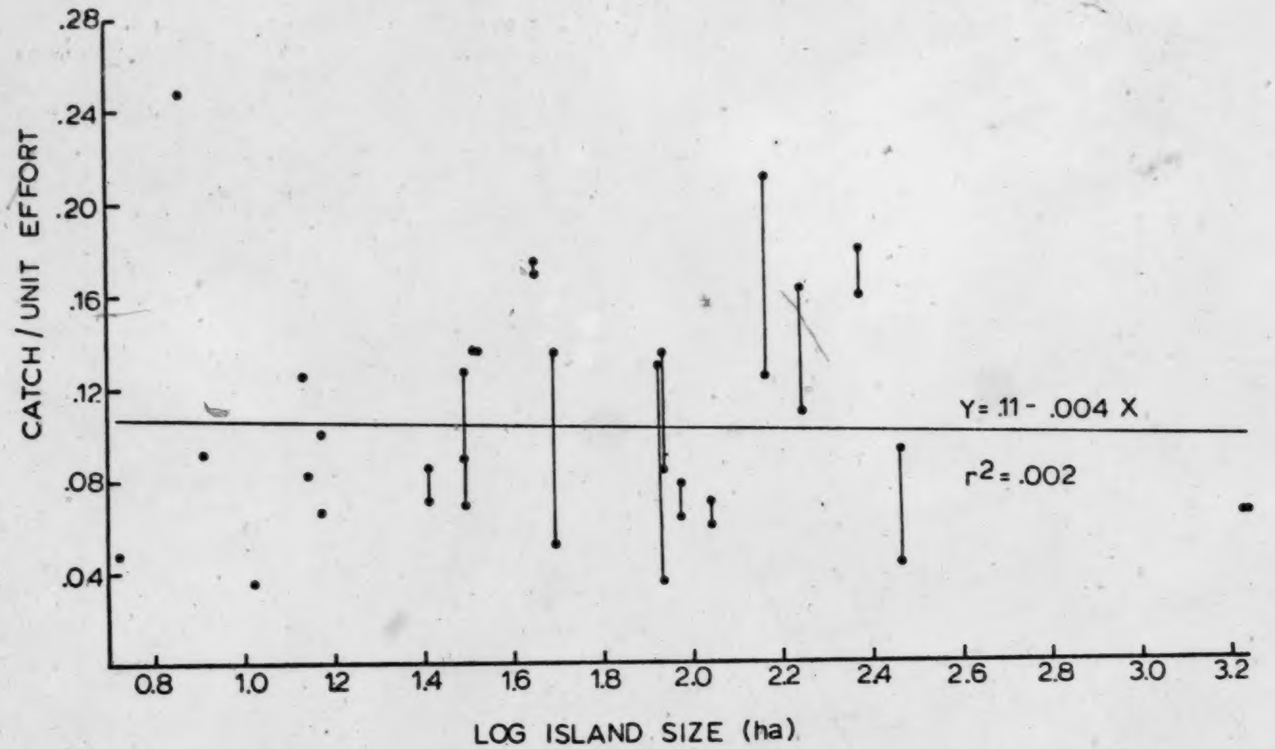


Figure 4. Relative abundance (catch per unit effort) of deermice (both sexes combined) in Barkley Sound in relation to island size; from 22 islands sampled during May-June 1977. Vertical lines join data from separate transects on a single island. Islands in order of increasing size: Fry, Keith, Erin, Walsh, Austin, Mullins, Chalk, Bauke, Prideaux, Sanford, Cooper, Willis, Jarvis, Dodd, Gibraltar, Edward King, Turtle, Nettle, Diana, Effingham, Fleming, Tzartus.

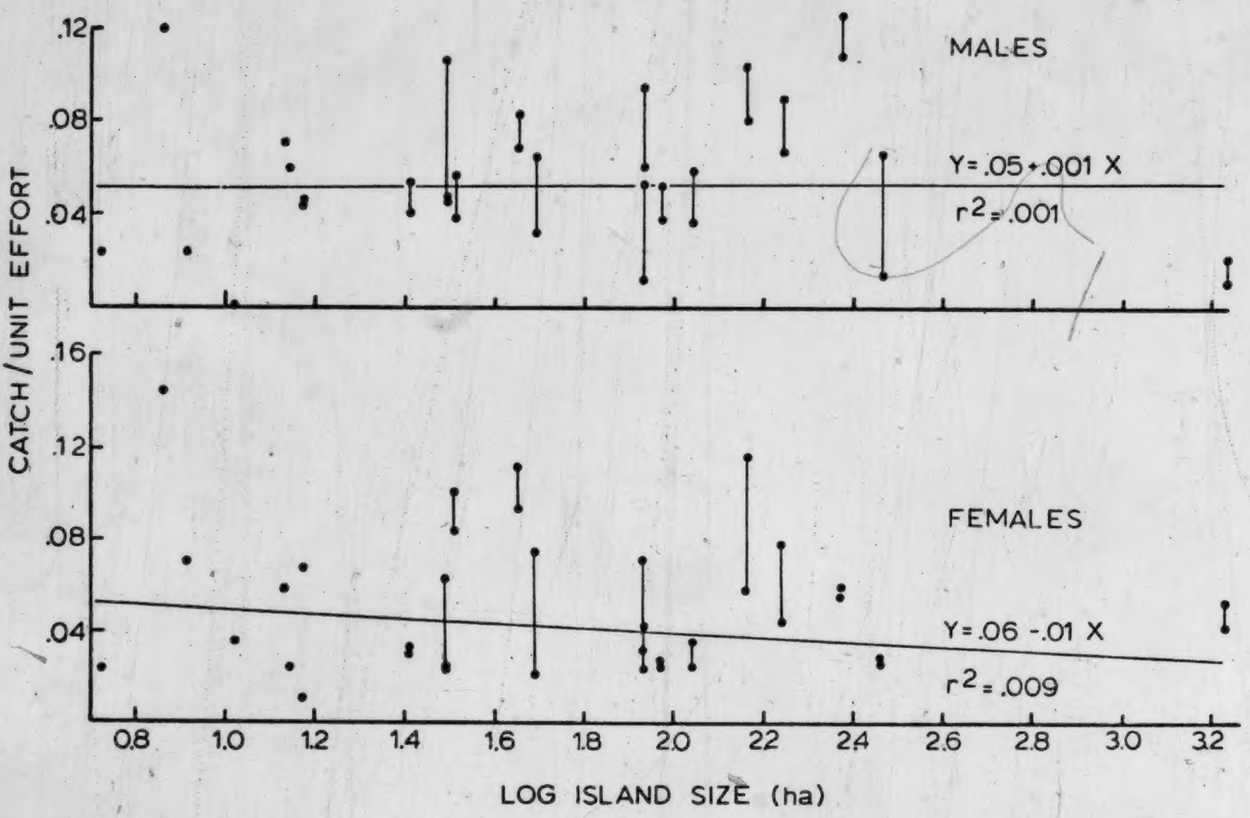
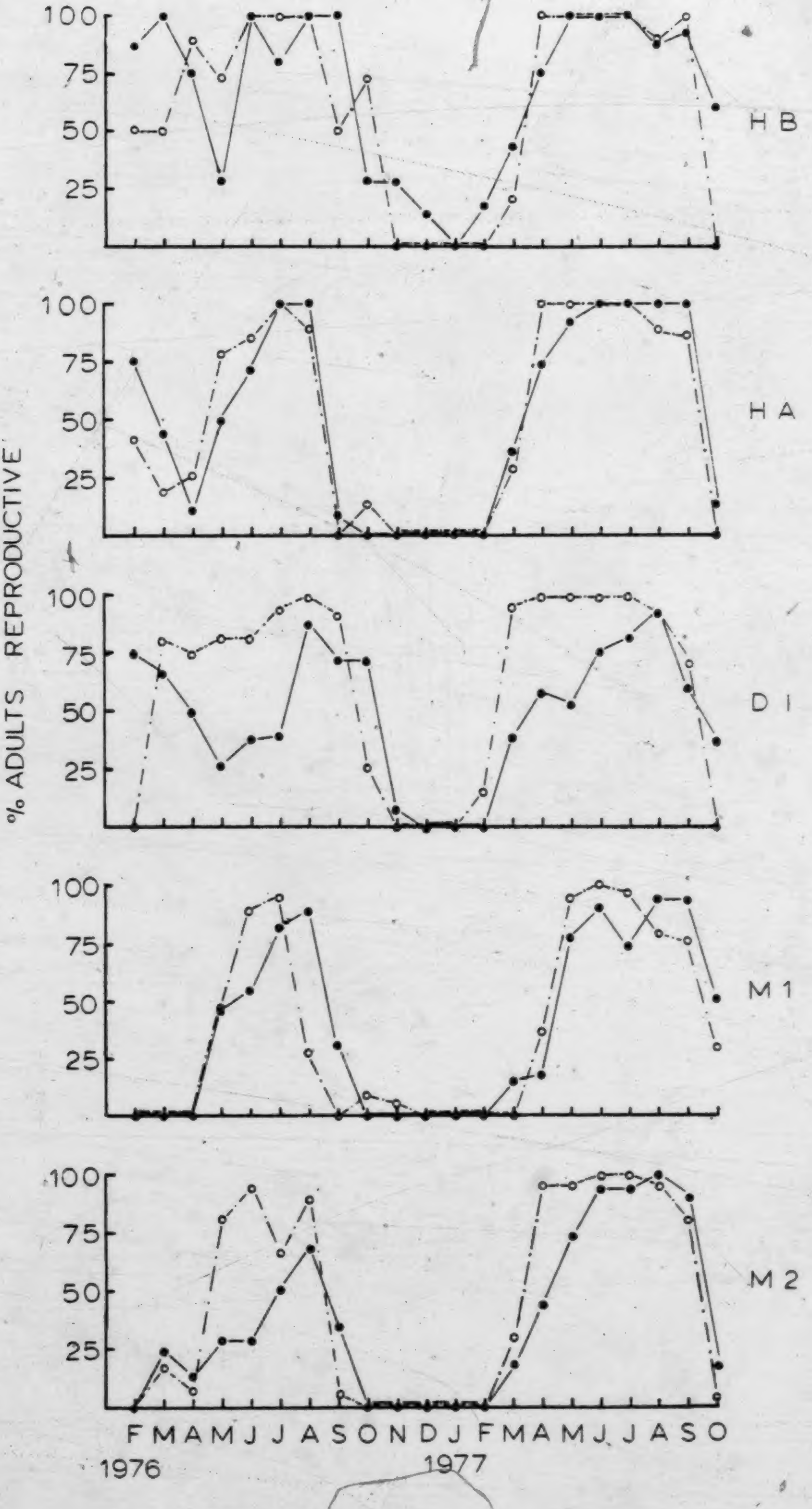


Figure 5. Relative abundance (catch per unit effort) of deermice (sexes separately) in Barkley Sound in relation to island size; from 22 islands sampled during May-June 1977. Vertical lines join data from separate transects on a single island. For identification of islands, see Figure 4.

Figure 6. Reproductive activity (expressed in percentage of adults reproductively active) on monthly live-trapping transects, from February 1976 to October 1977. HB = Helby Island, HA = Haines Island, DI = Diana Island, M1 = Mainland 1, M2 = Mainland 2, open circles = males, closed circles = females.


% ADULTS REPRODUCTIVE
100
75
50
25
H B
H A
D I
M 1
M 2
F
M
A
M
J
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O
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J
A
S
O
1976
1977

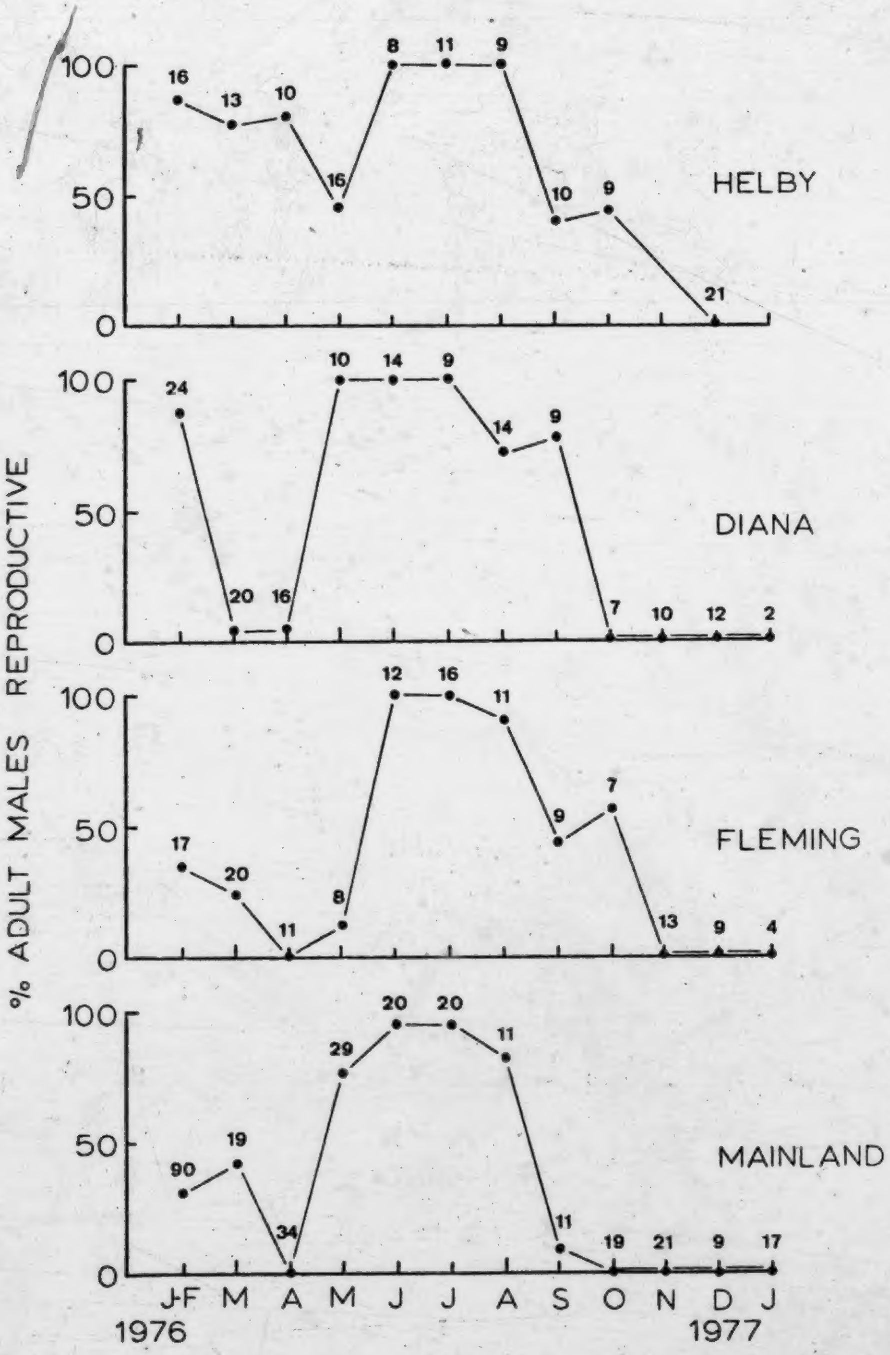


Figure 7. Reproductive activity of males (% of adult males reproductively active) in populations from monthly dead-trap samples, from January 1976 to January 1977. Total number of adults captured above data points.

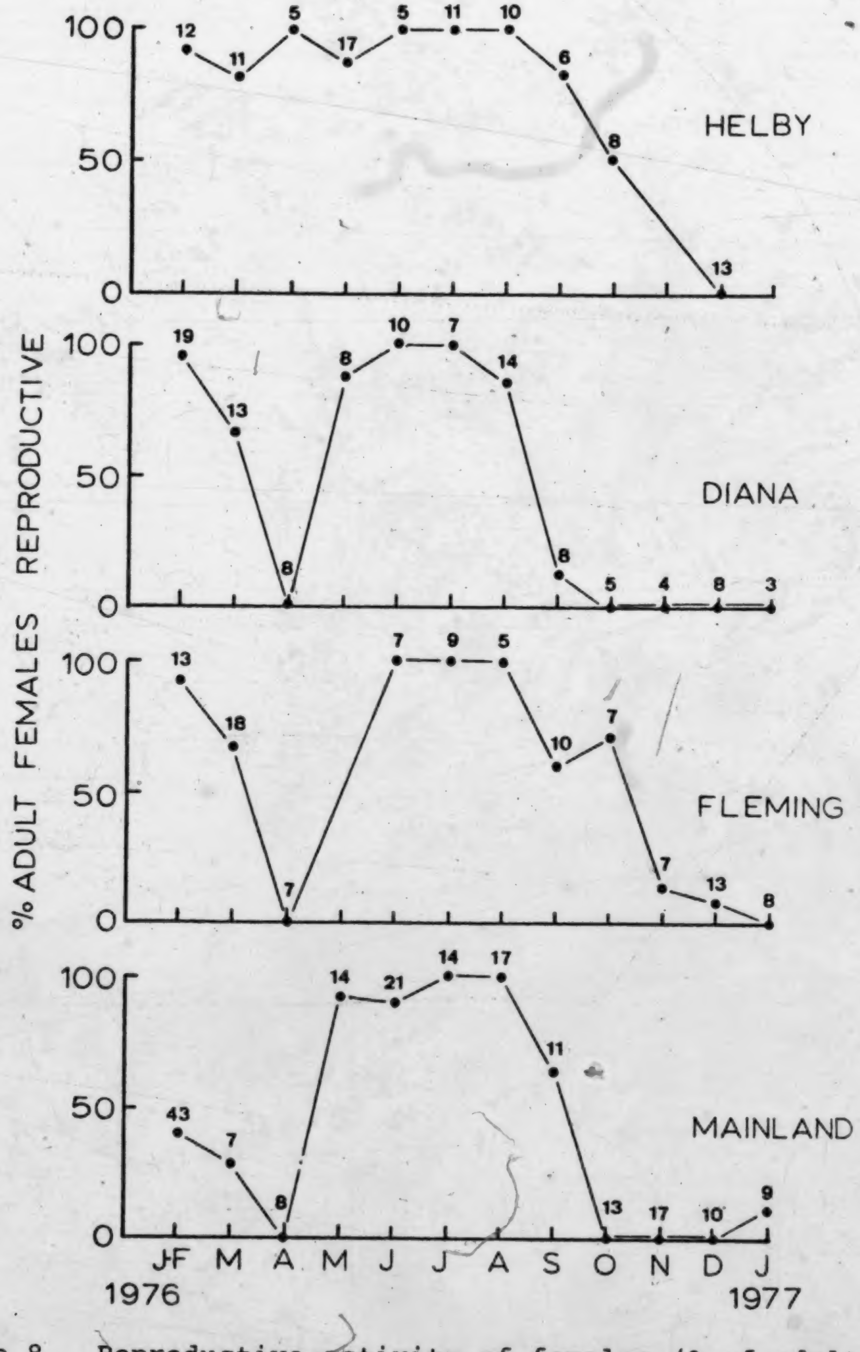


Figure 8. Reproductive activity of females (% of adult females reproductively active) in populations from monthly dead-trap samples, from January 1976 to January 1977. Total number of adults captured above data points.

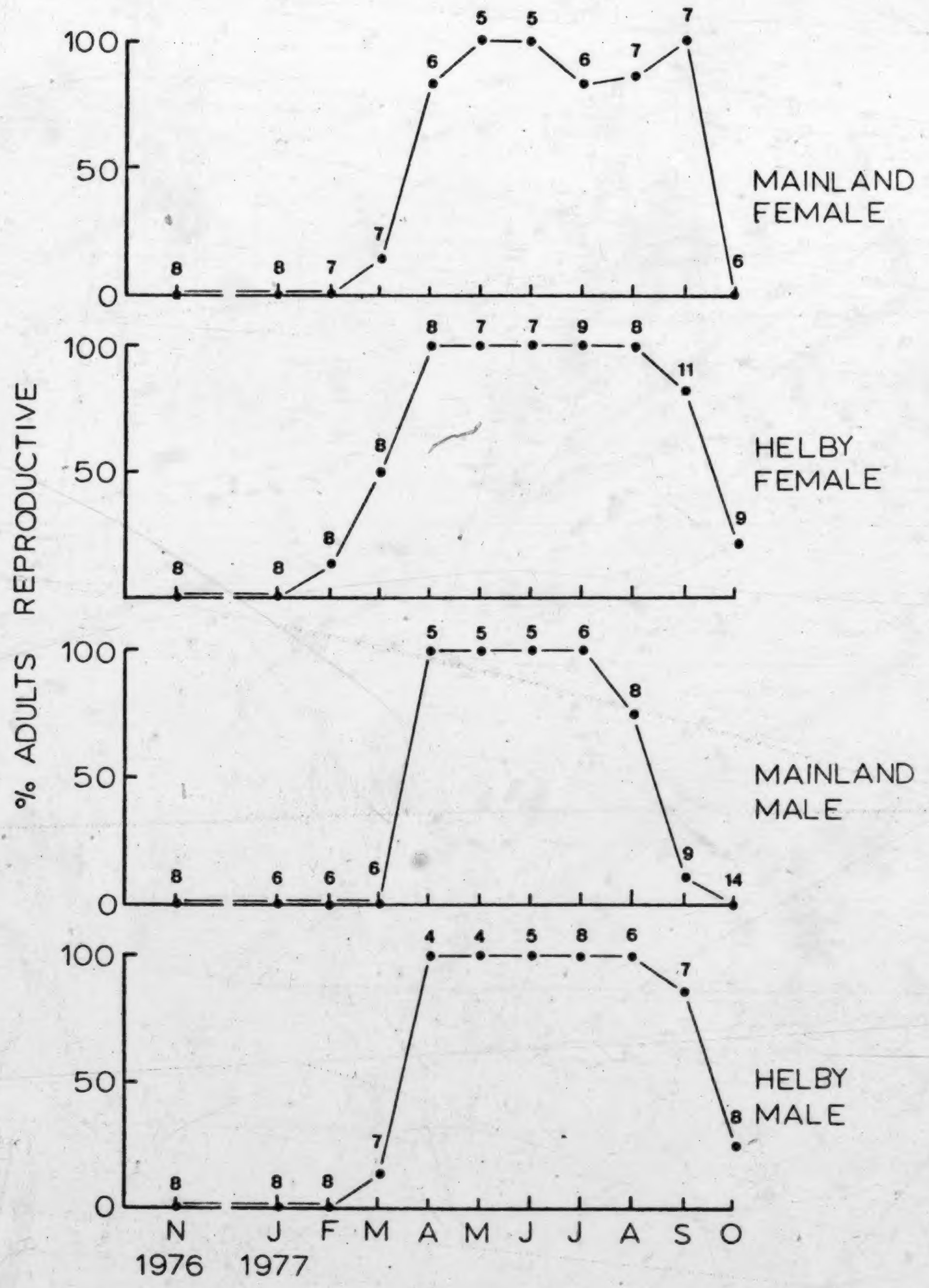
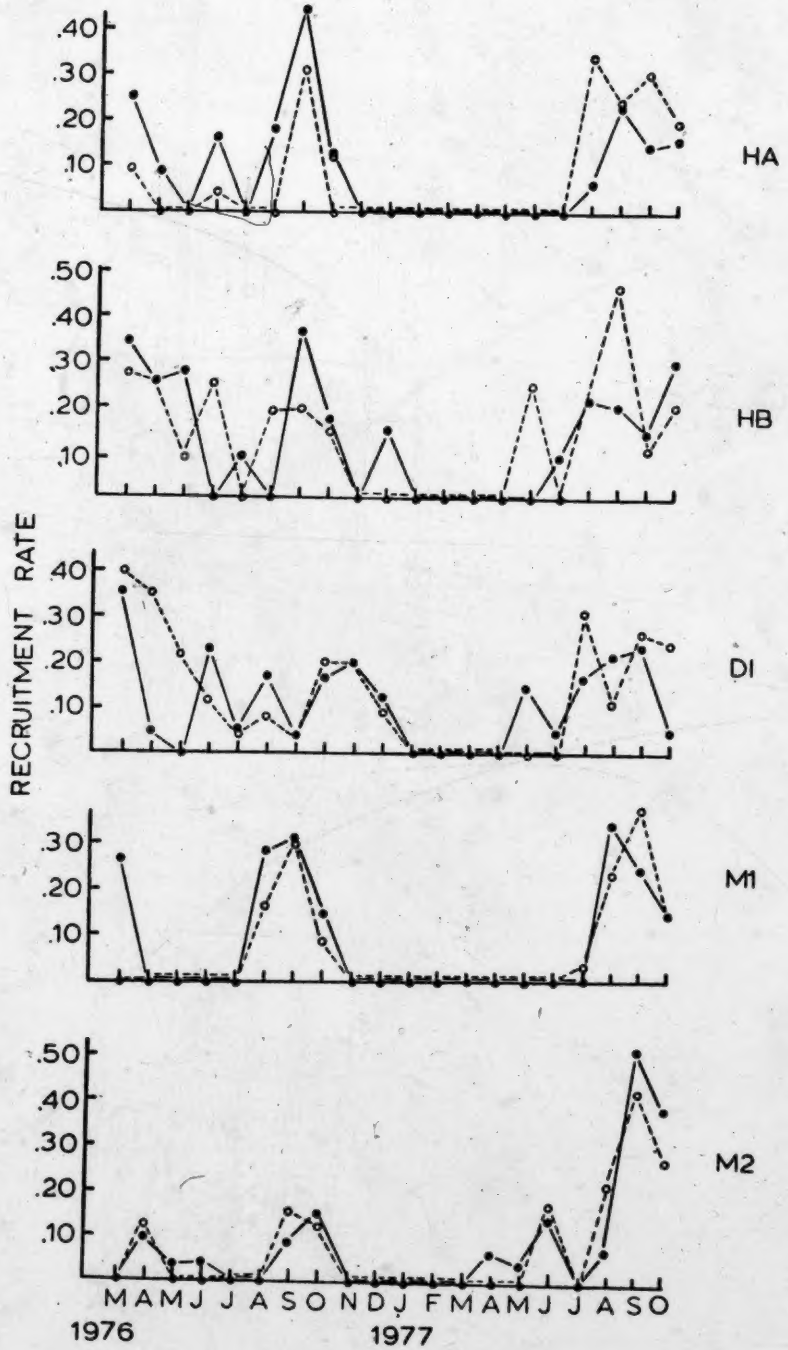


Figure 9. Reproductive activity (% of adults reproductively active) in island and mainland populations introduced to the Ross Islets. Number above data points represents total number of adults captured.

Figure 10. Recruitment of young deermice (expressed as percentage of total captures comprising unmarked juveniles and sub-adults) on monthly live-trapping transects. HA = Haines Island, HB = Helby Island, DI = Diana Island, M1 = Mainland 1, M2 = Mainland 2, open circles = males, closed circles = females.


RECRUITMENT RATE
.10
.20
.30
.40
.50
HA
HB
DI
M1
M2
M A M J J A S O N D J F M A M J J A S O
1976
1977

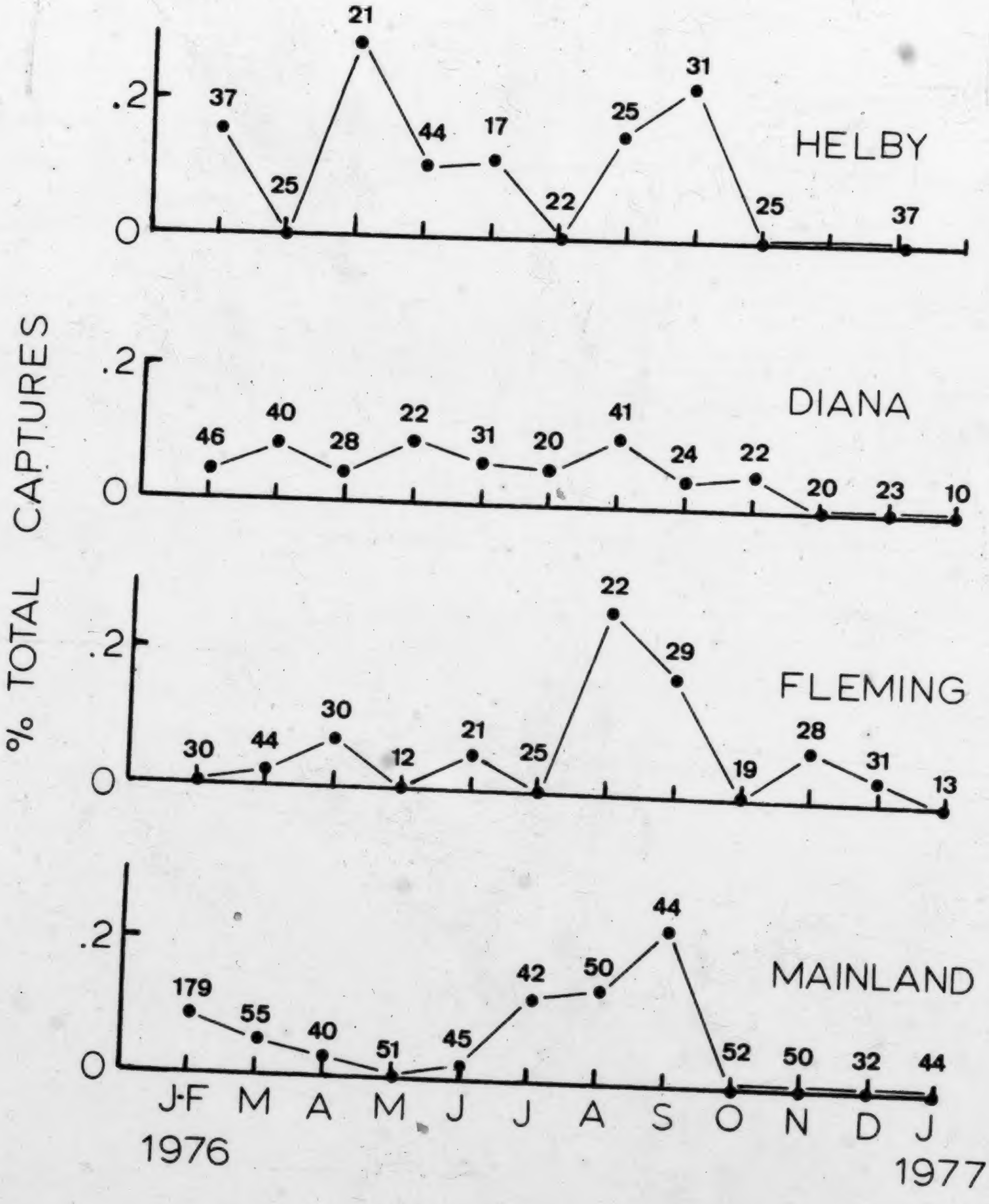


Figure 11. Percent composition of juveniles in monthly dead-trap samples from January 1976 to January 1977 for males and females combined. Total number of captures in each monthly sample above data points.

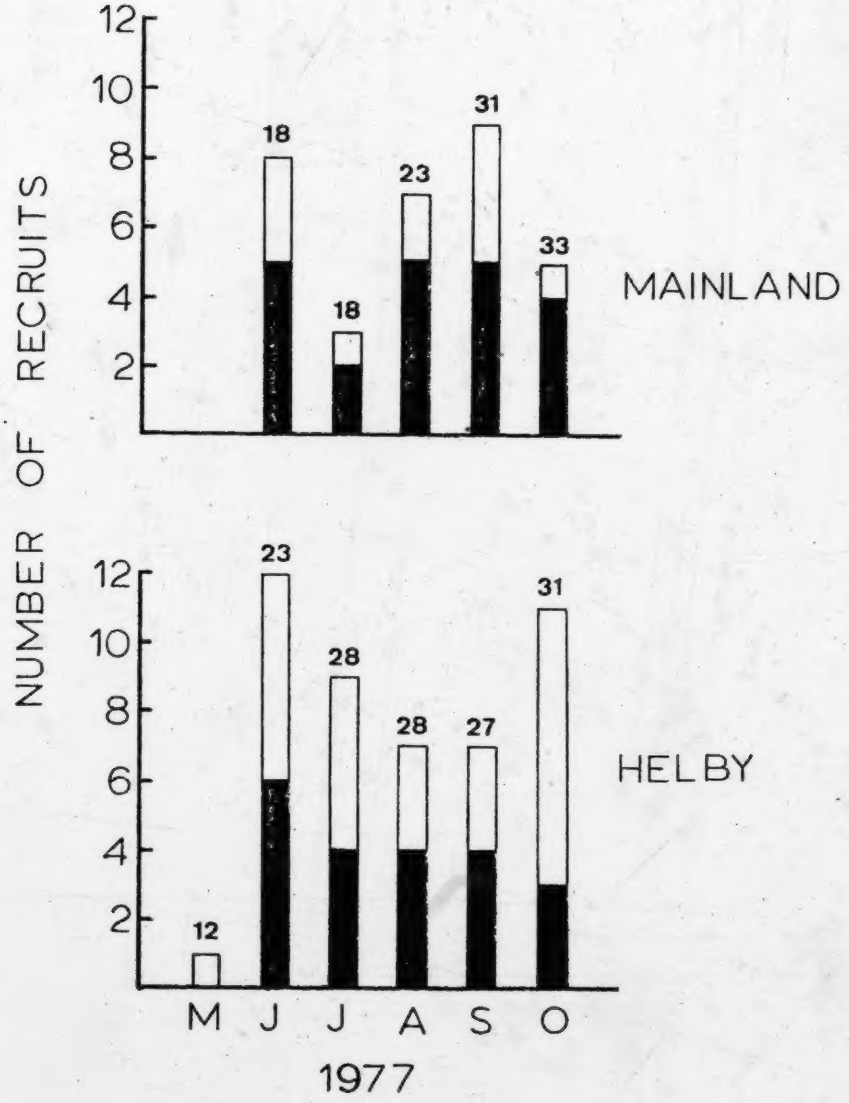


Figure 12. Recruitment in Helby Island and mainland stocks introduced to the Ross Islets. Minimum total population size above histograms. Shaded portions of histogram represent new males, unshaded portions new females.

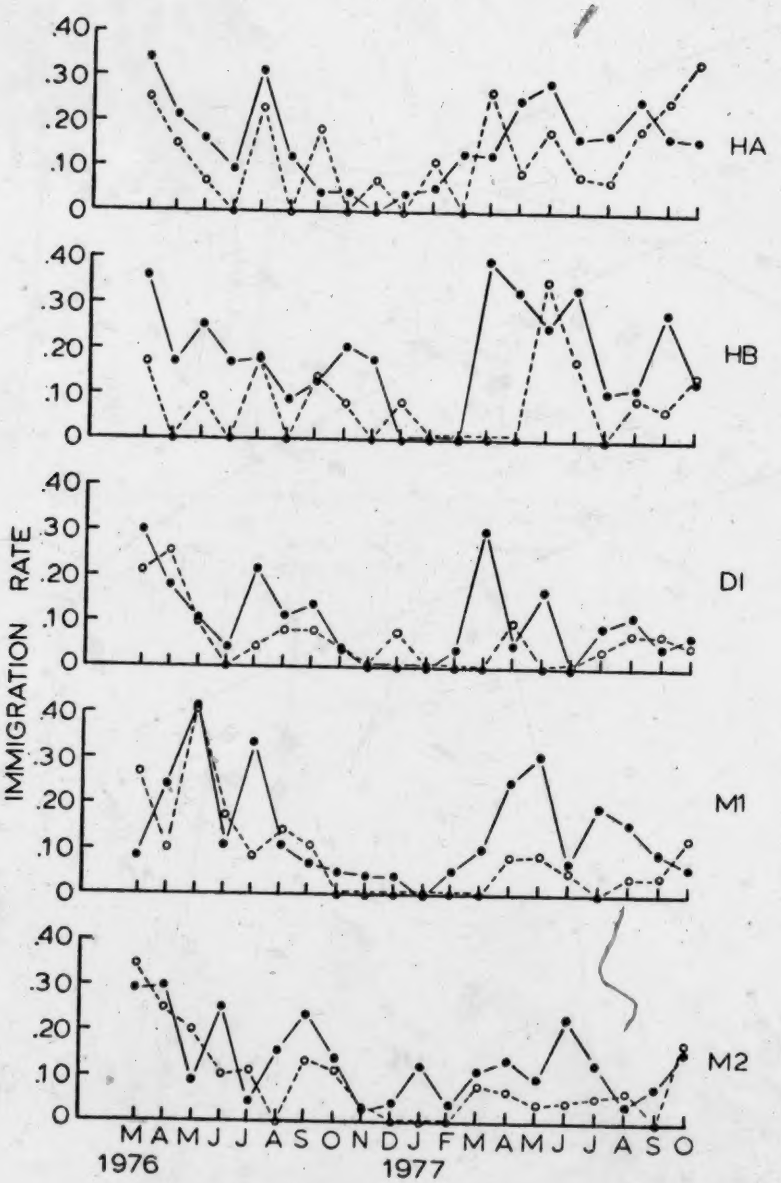
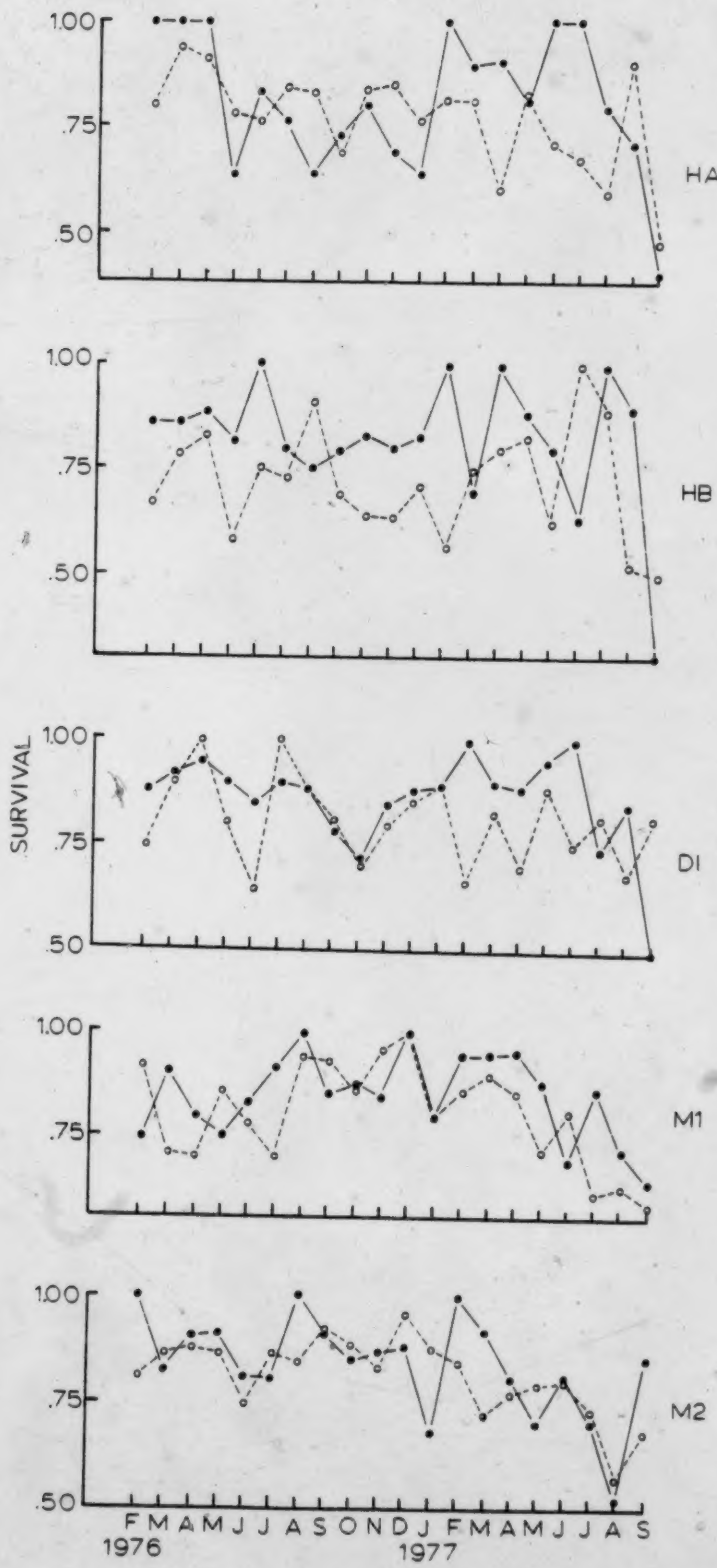


Figure 13. Adult immigration rates (number of unmarked adults/total number of captures) on monthly live-trapping transects, from March 1976 to October 1977. HA = Haines Island, HB = Helby Island, DI = Diana Island, M1 = Mainland 1, M2 = Mainland 2, closed circles = males, open circles = females.

Figure 14. Survival (number of mice captured in month n known to be alive in month n + 1/total number of mice captured in month n) on monthly live-trapping transects, from February 1976 to September 1977. HA = Haines Island, HB = Helby Island, DI = Diana Island, M1 = Mainland 1, M2 = Mainland 2, open circles = males, closed circles = females.


1.00
.75
.50
HA
1.00
.75
.50
HB
SURVIVAL
1.00
.75
.50
DI
1.00
.75
M1
1.00
.75
.50
M2
F M A M J J A S O N D J F M A M J J A S
1976
1977

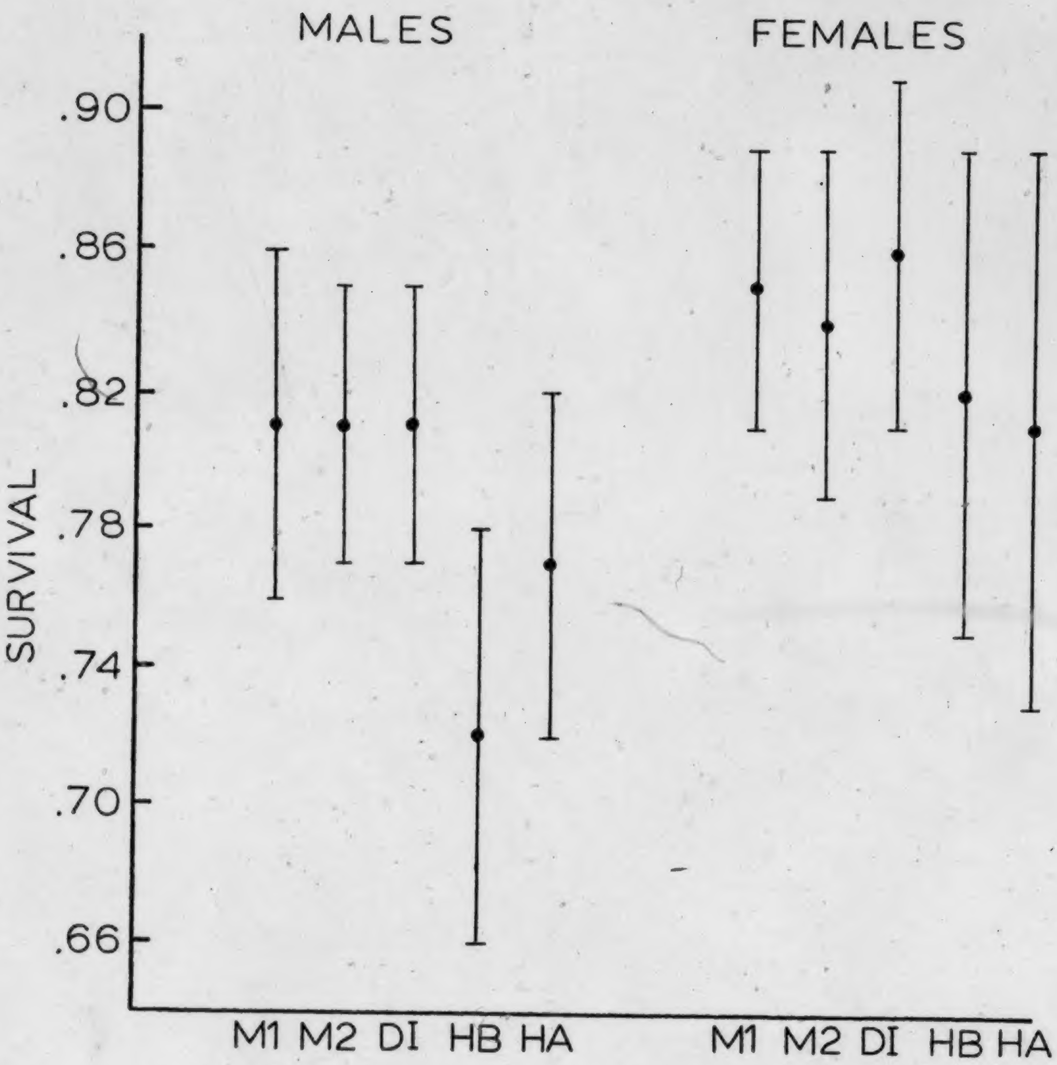


Figure 15. Mean survival (±2 s.e.) on monthly live-trapping transects (see text for details). M1 = Mainland 1, M2 = Mainland 2, DI = Diana Island, HB = Helby Island, HA = Haines Island, n = 20 for all groups.

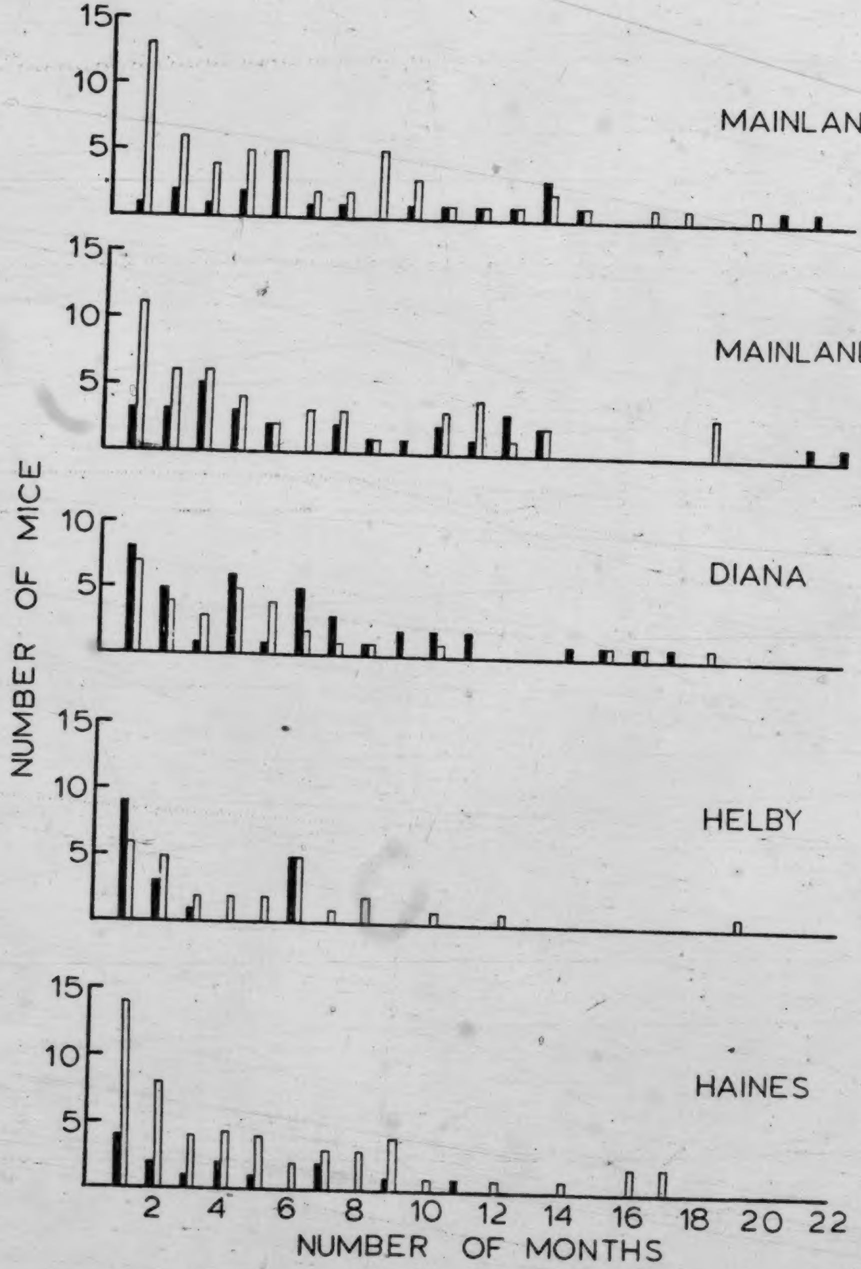


Figure 16. Length of life in male mice on live-trapping transects, according to age at first capture. Open bars include all mice first captured as adults; shaded bars include all mice first captured as sub-adults or juveniles. Only mice captured before June 1977 were included in analysis.

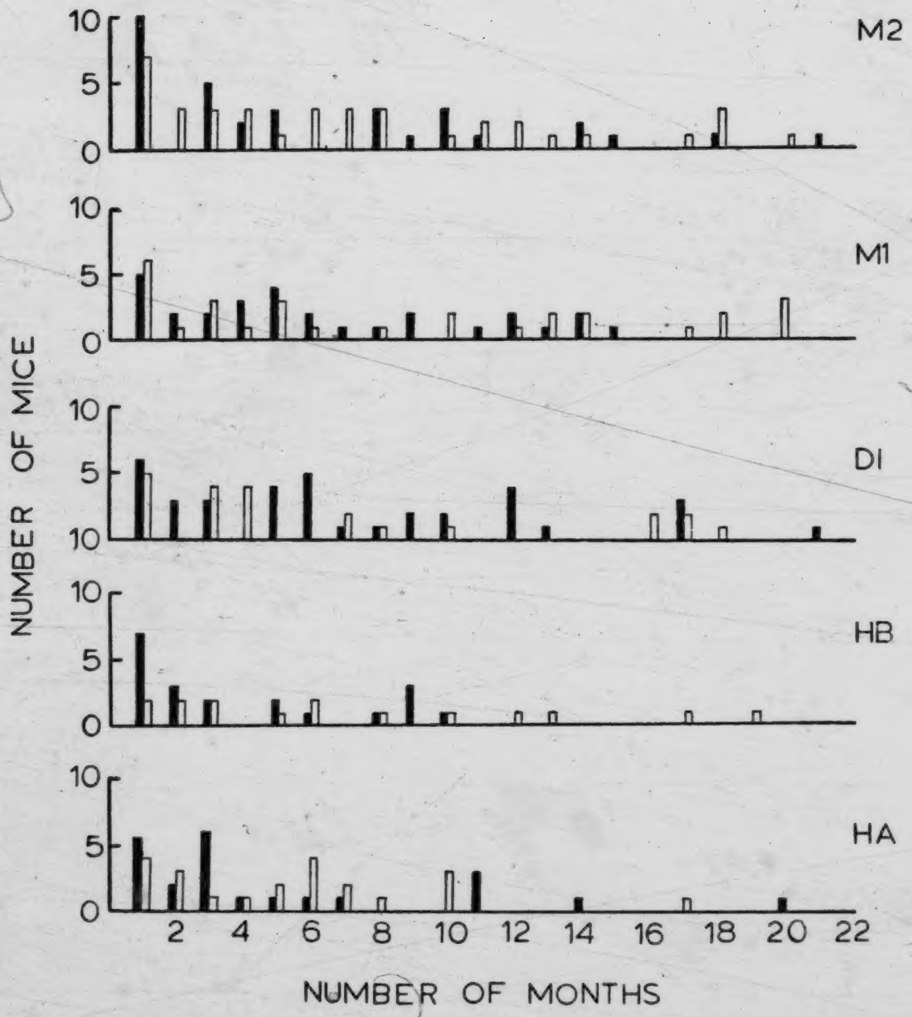


Figure 17. Length of life in female mice on live-trapping transects, according to age at first capture. Open bars include all mice first captured as adults; shaded bars include all mice first captured as sub-adults or juveniles. Only mice captured before June 1977 were included in the analysis. HA = Haines Island, HB = Helby Island, DI = Diana Island, M1 = Mainland 1, M2 = Mainland 2.

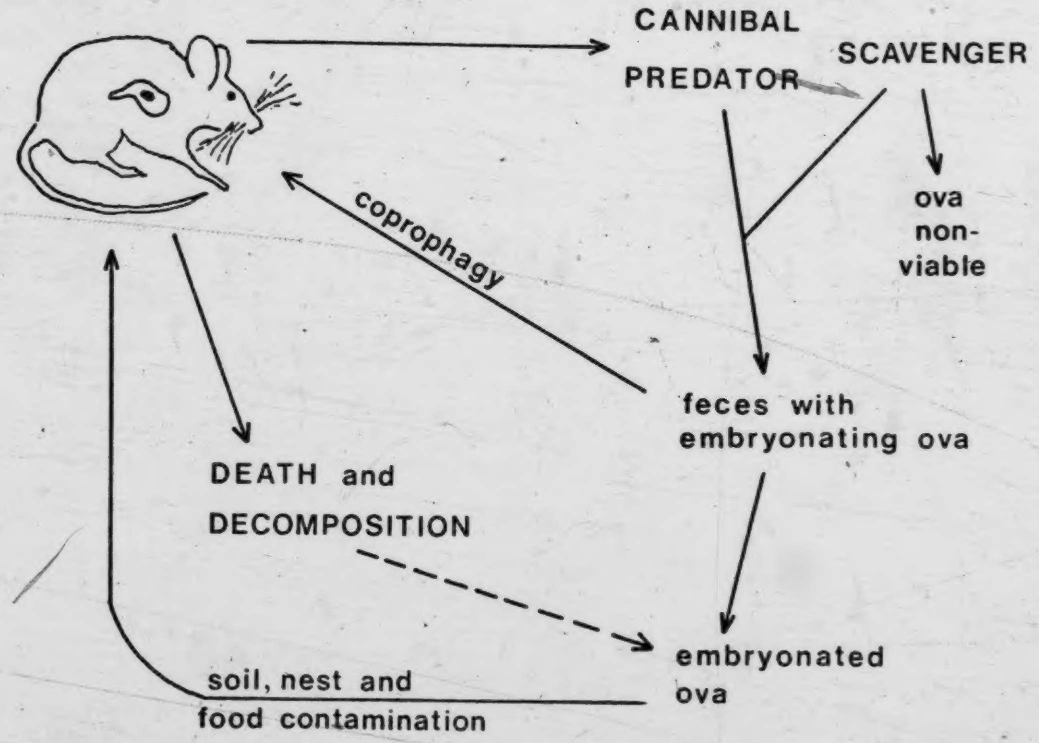

CANNIBAL
PREDATOR
SCAVENGER
ova
non-
viable
coprophagy
feces with
embryonating ova
DEATH and
DECOMPOSITION
embryonated
ova
soil, nest and
food contamination

Figure 18. Potential transmission pathways of the parasitic nematode *Capillaria hepatica*.

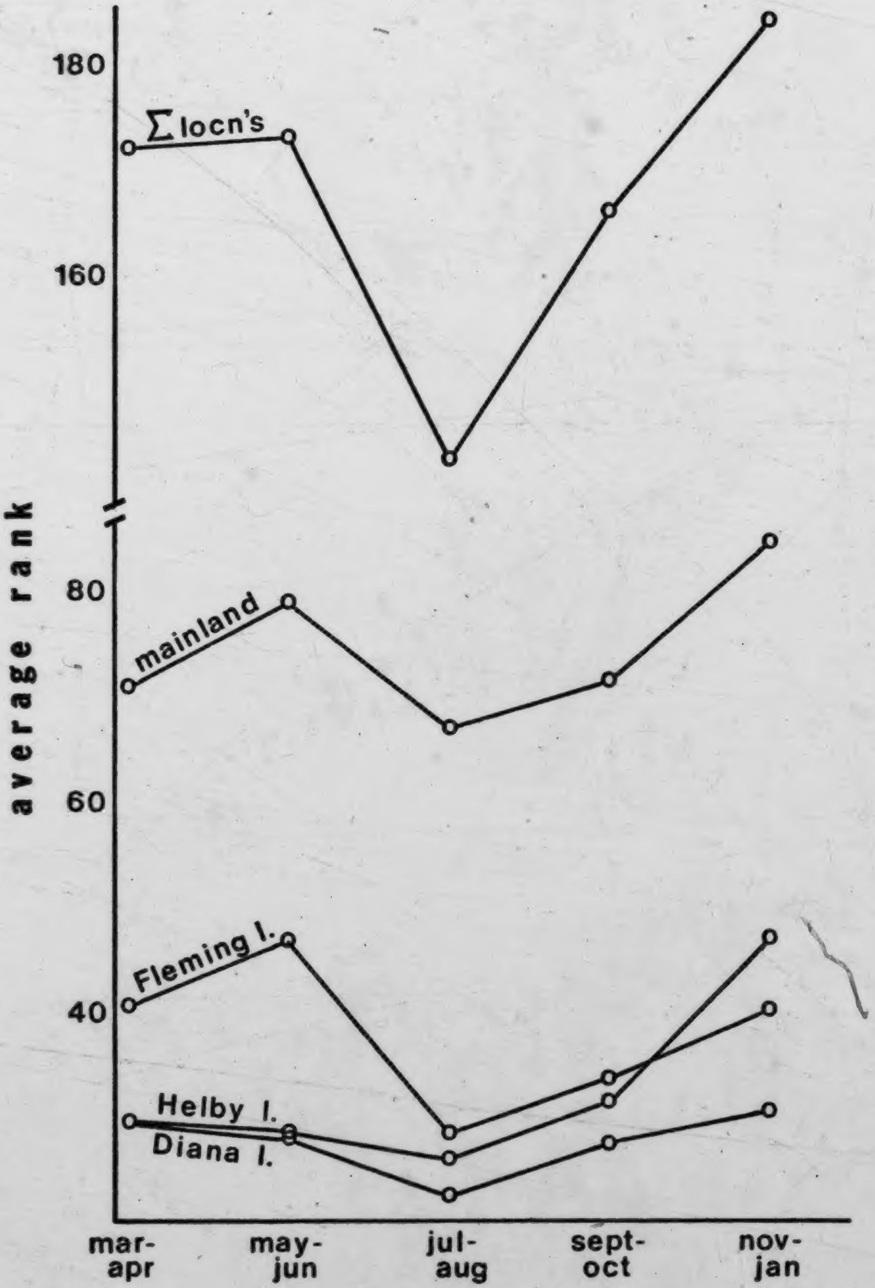


Figure 19. Seasonal patterns of *Capillaria hepatica* infections in young deermice expressed as the average rank of infection levels from Kruskal-Wallis ANOVA among seasons for each location (see text for details).

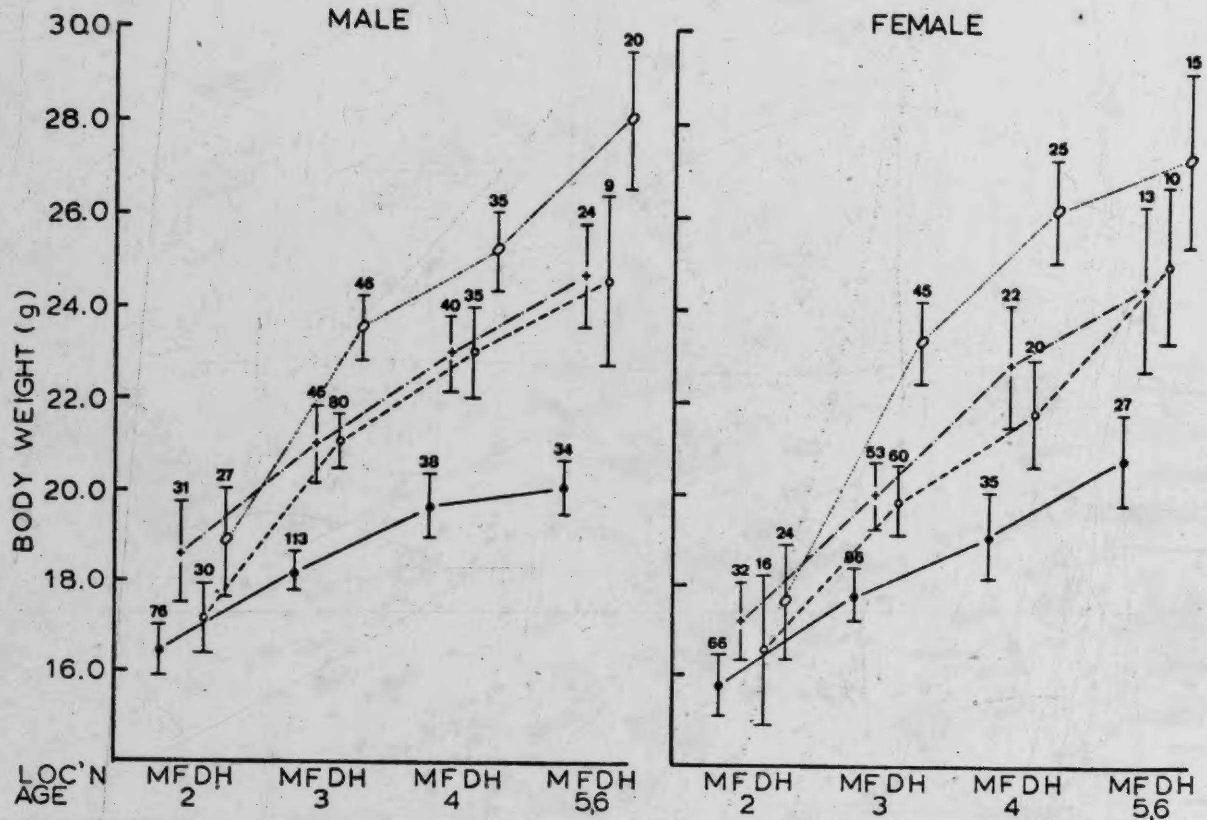
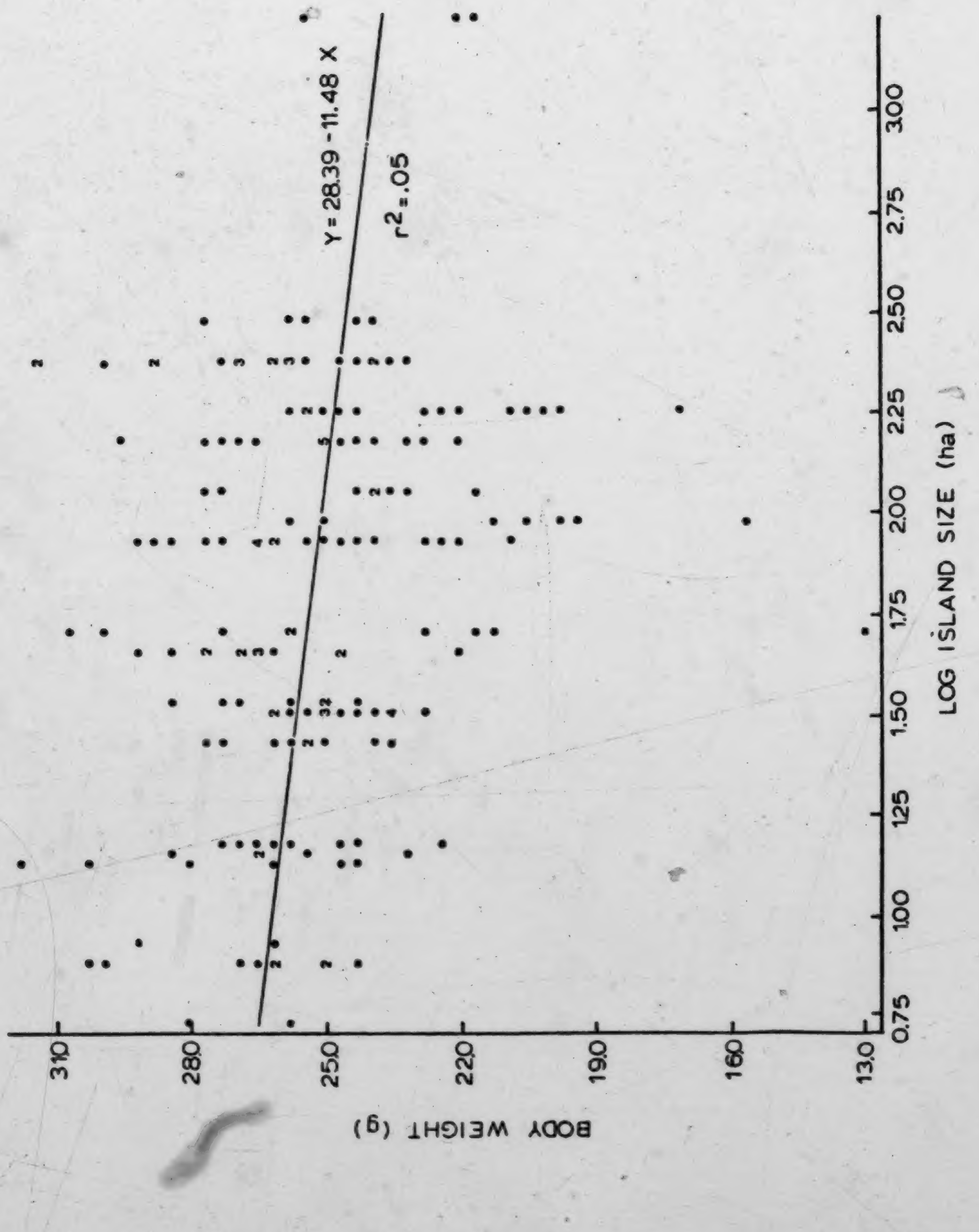
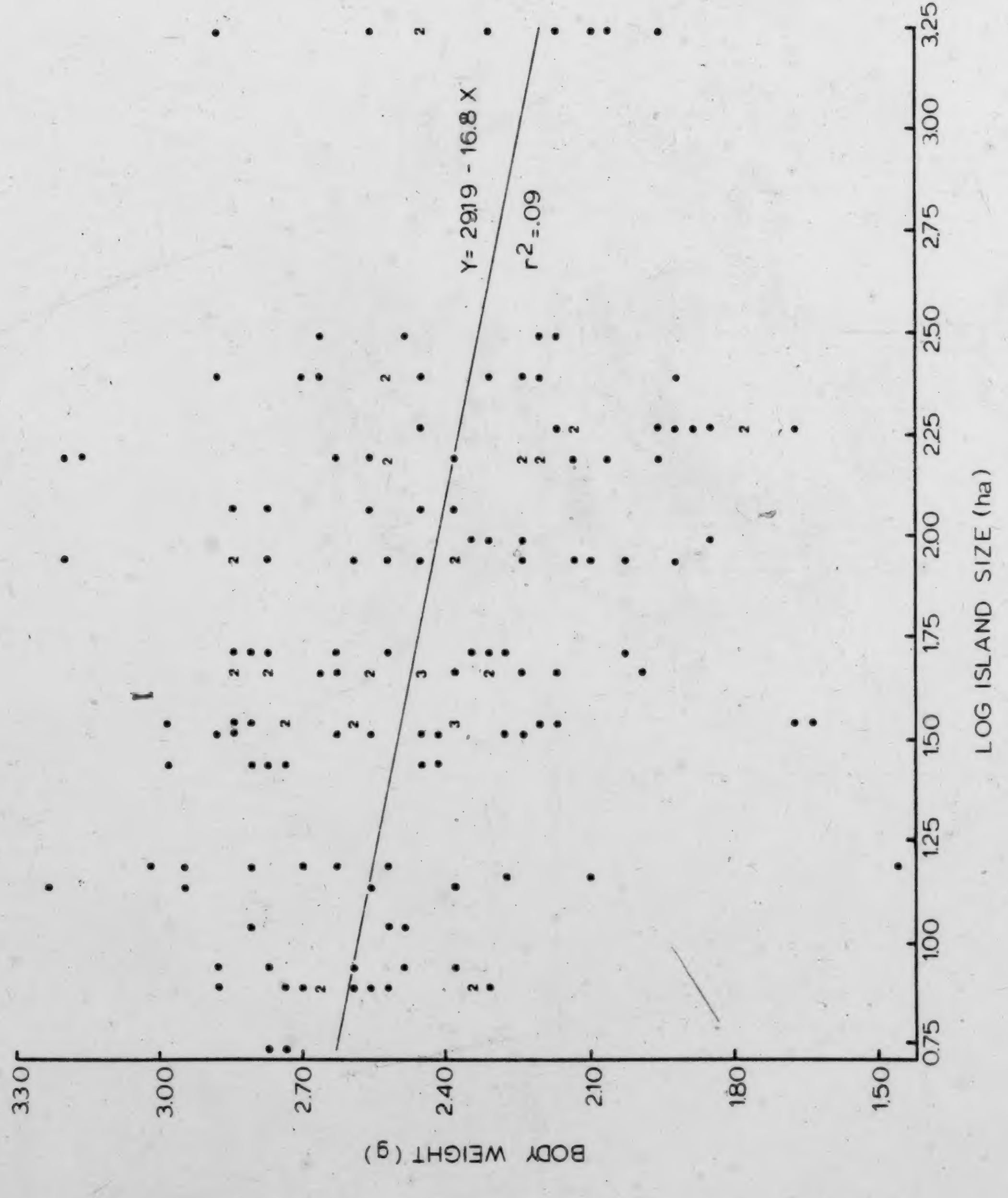


Figure 20. Mean body weight (±2 s.e.) of mice collected on monthly dead-trap transects, arrayed by age; samples from all months combined. Sample size above data points. M = mainland, F = Fleming Island, D = Diana Island, H = Helby Island.

Figure 21. Body weights of male mice in relation to island size, from 22 islands in Barkley Sound sampled during May-June 1977. For identification of islands, see Figure 4.


Y = 28.39 - 11.48 X
r^2 = .05
BODY WEIGHT (g)
31.0
28.0
25.0
22.0
19.0
16.0
13.0
LOG ISLAND SIZE (ha)
0.75
1.00
1.25
1.50
1.75
2.00
2.25
2.50
2.75
3.00


BODY WEIGHT (g)
3.30
3.00
2.70
2.40
2.10
1.80
1.50
0.75
1.00
1.25
1.50
1.75
2.00
2.25
2.50
2.75
3.00
3.25
LOG ISLAND SIZE (ha)
Y= 29.19 - 16.8 X
r2 =.09

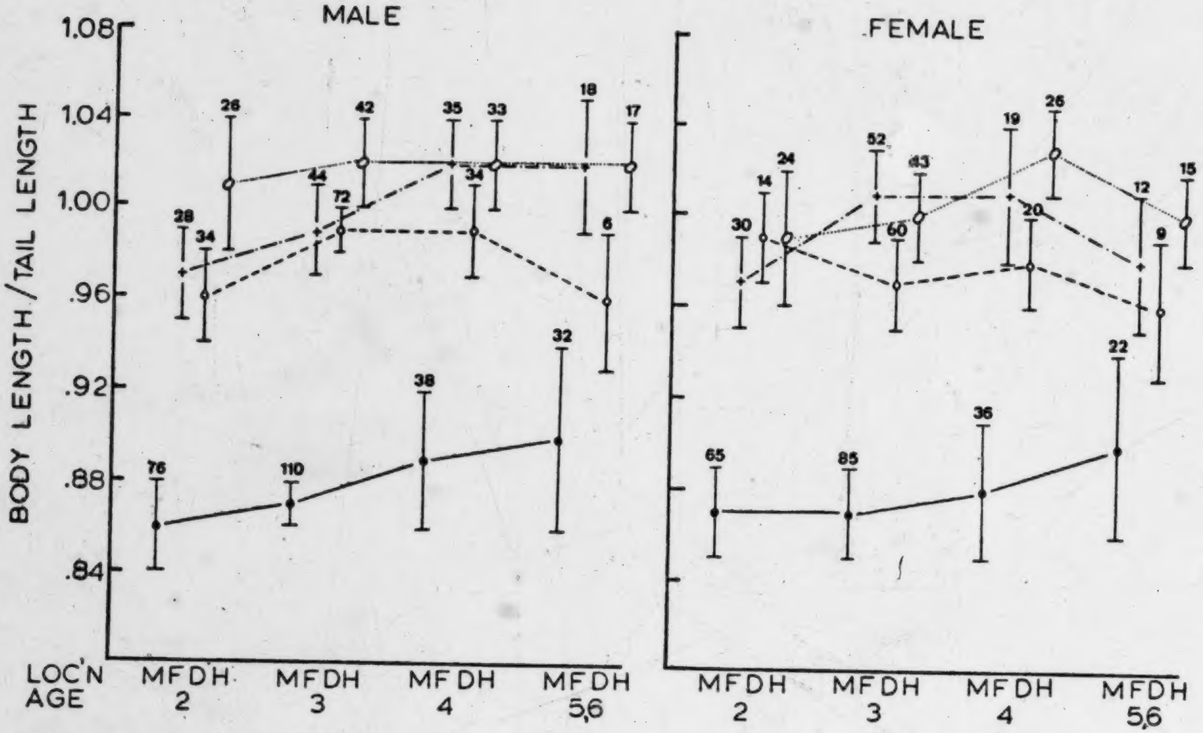


Figure 23. Mean body length/tail length ratios (±2 s.e.) of mice collected on monthly dead-trap transects, arrayed by age; samples from all months combined. Sample sizes above data apoints. M = mainland, F = Fleming Island, D = Diana Island, H = Helby Island.

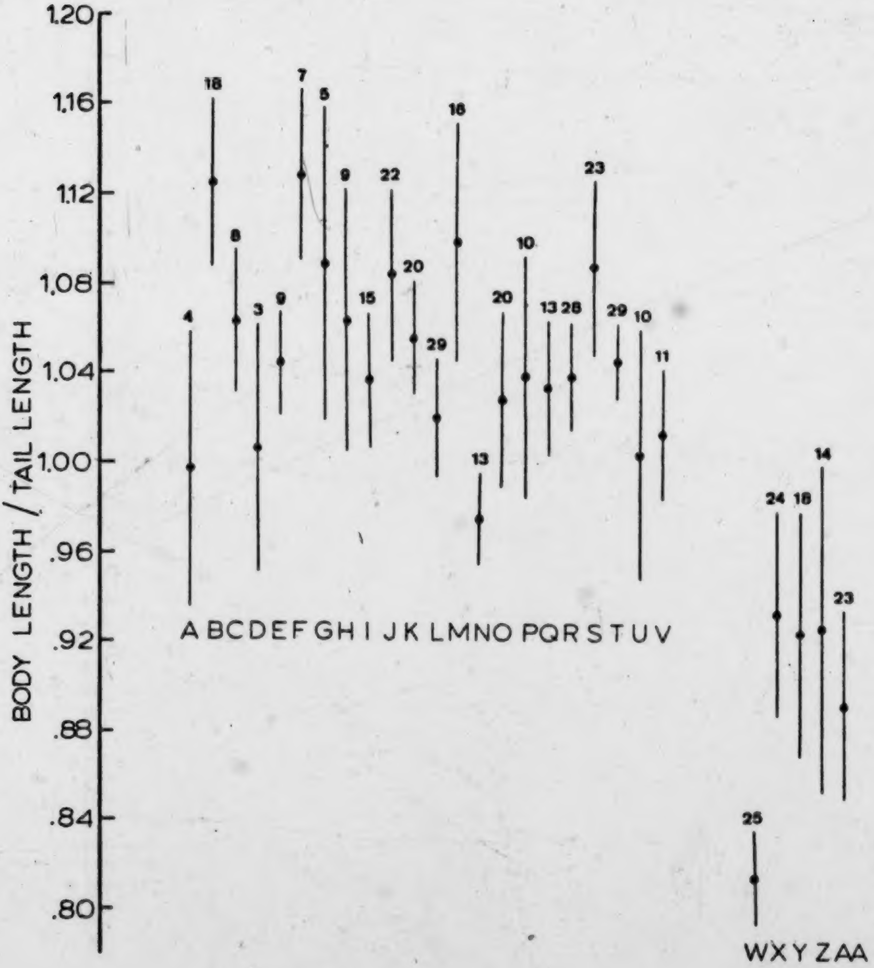


Figure 24. Mean body length/tail length ratios (±2 s.e.) of mice collected from 22 islands in Barkley Sound and from 5 mainland locations on adjacent Vancouver Island in May-June 1977. Sample sizes above data points. Islands arrayed in order of increasing size: A - Fry, B - Keith, C - Erin, D - Walsh, E - Austin, F - Mullins, G - Chalk, H - Bauke, I - Prideaux, J - Sanford, K - Cooper, L - Willis, M - Jarvis, N - Dodd, O - Gibraltar, P - Edward King, Q - Turtle, R - Nettle, S - Diana, T - Effingham, U - Fleming, V - Tzartus; W, X, Y, Z, AA - mainland.

LITERATURE CITED

Armitage, K. B., D. Johns, and D. C. Andersen. 1979. Cannibalism among yellow-bellied marmots. J. Mammal. 60: 205-207.

Avise, J. C., M. H. Smith, and R. K. Selander. 1979. Biochemical polymorphism and systematics in the genus *Peromyscus*. VII. Geographic differentiation in members of the *truei* and *maniculatus* species groups. J. Mammal. 60: 177-192.

Bailey, N. T. J. 1959. Statistical Methods in Biology. English Universities Press, London.

Bendell, J. F. 1959. Food as a control of a population of white-footed mice, *Peromyscus leucopus noveboracensis* (Fischer). Can. J. Zool. 37: 173-209.

Berry, R. J. 1964. The evolution of an island population of the house mouse. Evolution 18: 468-483.

Blair, W. F. 1951. Population structure, social behaviour and environmental relations in a natural population of the beach mouse (*Peromyscus polionotus*). Contrib. Lab. Vert. Biol., Univ. of Michigan 48: 1-47.

Boice, R. 1972. Some behavioral tests of domestication in Norway rats. Behavior 42: 198-231.

Bourlière, F. 1957. Ageing and metabolism. In W. B. Yapp and G. H. Bourne, eds. The biology of ageing. Symp. Inst. Biol. 6: 27-34.

Brant, D. H. 1962. Measures of the movements and population densities of small rodents. Univ. Calif. Publ. Zool. 62: 105-184.

Bujalska, G. 1973. The role of spacing behaviour among females in the regulation of reproduction in the bank vole. J. Reprod. Fert., Suppl. 19 (1973): 465-474.

________________. 1975. Reproduction and mortality of bank voles and the changes in the size of an island population. Acta Theriol. 20: 41-56.

Canfield, R. 1941. Application of the line interception method in sampling range vegetation. J. Forestry 39: 388-394.

Canham, R. P. 1969. Early cessation of reproduction in an unusually abundant population of *Peromyscus maniculatus borealis*. Can. Field-Naturalist 83: 279.

________________. 1970. Sex ratios and survival in fluctuating populations of the deer mouse, *Peromyscus maniculatus borealis*. Can. J. Zool. 48: 809-811.

Carlquist, S. 1965. Island Life. Natural History Press, New York.

________________. 1971. Introduction. In Stern, W. L. (ed.). Adaptive aspects of insular evolution. Wash. St. Univ. Press, Pullman.

________________. 1974. Island Biology. Columbia Univ. Press, New York.

Carter, L. 1971. Surficial sediments of Barkley Sound and adjacent continental shelf, Vancouver Island, British Columbia. Ph.D. Dissertation, Univ. of British Columbia.

Case, T. J. 1978. A general explanation for insular body size trends in terrestrial vertebrates. Ecology 59: 1-18.

Charnov, E. L. and W. M. Schaffer. 1973. Life history consequences of natural selection: Cole's result revisited. Am. Nat. 107: 791-793.

Clough, G. C. 1969. The Bahaman hutia: a rodent refound. Oryx 10: 106-108.

Cook, L. M. 1961. The edge effect in population genetics. Am. Nat. 95: 295-307.

Corbet, G. B. 1961. Origin of the insular races of small mammals and the "Lusitanian" fauna. Nature 191: 1037-1040.

Coutts, R. R. and I. W. Rowlands. 1969. The reproductive cycle of the Skomer vole (*Clethrionomys glareolus skomerensis*). J. Zool. (Lond.) 158: 1-25.

Craighead, J. J. and F. C. Craighead. 1956. Hawks, Owls and Wildlife. Stackpole, Harrisburg, Pa.

Crowell, K. L. 1962. Reduced interspecific competition among the birds of Bermuda. Ecology 43: 75-88.

_______________. 1973. Experimental zoogeography: Introduction of mice to small islands. Am. Nat. 107: 535-558.

Darwin, C. 1859. The origin of species by means of natural selection. John Murray, London.

Deevey, E. S. 1947. Life tables for natural populations of animals. Q. Rev. Biol. 22: 283-314.

Delany, M. J. 1961. The ecological distribution of small mammals in North-West Scotland. Proc. Zool. Soc. Lond. 137: 107-126.

_______________. 1970. Variation and ecology of island populations of the long-tailed field mouse (*Apodemus sylvaticus*). Symp. Zool. Soc. Lond. 26: 283-295.

Eisenberg, J. F. 1968. Behavior patterns. In J. A. King (ed.), Biology of *Peromyscus*. Am. Soc. Mammal. Special Publ. No. 2, pp. 451-495.

Fairbairn, D. 1976. The spring decline in deer mice: death or dispersal. Can. J. Zool. 55: 84-92.

_______________. 1977. Why breed early? A study of reproductive tactics in *Peromyscus*. Can. J. Zool. 55: 862-871.

_______________. 1978. Behavior of dispersing deer mice (*P. maniculatus*). Behav. Ecol. Sociobiol. 3: 265-282.

Farhang-Azad, A. 1977a. Ecology of *Capillaria hepatica* (Bancroft 1893) (Nematoda). I. Dynamics of infection among Norway rat populations of the Baltimore zoo, Baltimore, Maryland. J. Parasit. 63: 117-122.

_______________. 1977b. Ecology of *Capillaria hepatica* (Bancroft 1893) (Nematoda). II. Egg-releasing mechanisms and transmission. J. Parasit. 63: 701-706.

Flowerdew, J. R. 1972. The effect of supplementary food on a population of wood mice (*Apodemus sylvaticus*). J. Anim. Ecol. 42: 553-566.

Fordham, R. A. 1971. Field populations of deermice with supplemental food. Ecology 52: 138-146.

Foster, J. B. 1965. The evolution of the mammals of the Queen Charlotte Islands, British Columbia. Occas. Pap. British Columbia Prov. Mus. No. 14. 130pp.

Fox, L. R. 1975. Cannibalism in natural populations. Ann. Rev. Ecol. and Syst. 6: 87-106.

Freeman, R. S. and K. A. Wright. 1960. Factors concerned with the epizootiology of *Capillaria hepatica* in a population of *Peromyscus maniculatus* in Algonquin Park, Canada. Can. J. Zool. 38: 373-382.

Fullaghar, P. J., P. A. Jewell, R. M. Lockley, and I. W. Rowlands. 1963. The Skomer vole (*Clethrionomys glareolus skomerensis*) on Skomer Island, Pembrokeshire in 1960. Proc. Zool. Soc. Lond. 140: 295-314.

Garten, C. T., Jr. 1976. Relationships between aggressive behavior and genic heterozygosity in the oldfield mouse, *Peromyscus polionotus*. Evolution 30: 59-72.

Grant, P. R. 1965. The adaptive significance of some size trends in island birds. Evolution 19: 255-267.

Guiguet, C. J. 1974. A qualitative inventory of insular mammalian faunas from the west coast of Vancouver Island. Syesis 7: 71-77.

Halpin, Z. T. and T. P. Sullivan. 1978. Social interactions in island and mainland populations of the deer mouse, *Peromyscus maniculatus*. J. Mammal. 59: 395-401.

Hatler, D. F. 1976. The coastal mink on Vancouver Island, British Columbia. Ph.D. Dissertation, Univ. of British Columbia.

Healey, M. C. 1967. Aggression and self-regulation of population size in deer mice. Ecology 48: 377-392.

Heaney, L. R. 1978. Island area and body size of insular mammals: evidence from the tri-colored squirrel (*Callosciurus prevosti*) of southeast Asia. Evolution 32: 29-44.

Hitchcock, C. L. and A. Cronquist. 1973. Flora of the Pacific Northwest. Univ. of Washington Press, Seattle.

Hoffman, R. S. 1955. A population high for *Peromyscus maniculatus*. J. Mammal. 36: 571-572.

Holmes, W. G. 1977. Cannibalism in the arctic ground squirrel (*Spermophilus parryii*). J. Mammal. 58: 437-438.

Jewell, P. A. 1966. Breeding season and recruitment in some British mammals confined on small islands. Symp. Zool. Soc. Lond. 15: 89-116.

Kavanau, J. L. 1967. Behavior of captive white-footed mice. Science 155: 1623-1639.

Kramer, G. 1946. Veranderungen von Nachkommenziffer und Nachkommengrosse sowie der Altersverteilung von inseleidechsen. Z. Naturforsch. 1: 700-710.

________________. 1951. Body proportions of mainland and island lizards. Evolution 5: 193-206.

Krebs, C. J., B. L. Keller, and R. H. Tamarin. 1969. *Microtus* population biology: demographic changes in fluctuating populations of *M. ochrogaster* and *M. pennsylvanicus* in southern Indiana. Ecology 50: 587-607.

Lack, D. 1971. Island birds. In Stern, W. L. (ed.), Adaptive aspects of insular evolution. Wash. St. Univ. Press, Pullman.

Layne, J. N. 1968. Host and ecological relationships of the parasitic helminth *Capillaria hepatica* in Florida mammals. Zoologica 53: 107-123.

Lidicker, W. Z., Jr. 1962. Emigration as a possible mechanism permitting the regulation of population density below carrying capacity. Am. Nat. 96: 29-33.

________________. 1975. The role of dispersal in the demography of small mammals. In Golley, F. B., K. Petrusewicz and L. Ryszkowski (eds.), Small Mammals: productivity and dynamics of populations. Cambridge Univ. Press, London. pp. 105-128.

Luttermoser, G. W. 1938. An experimental study of *Capillaria hepatica* in the rat and the mouse. Amer. J. Hyg. 27: 321-340.

MacArthur, R. H. 1972. Geographical Ecology. Harper and Row, New York.

MacArthur, R. H. and E. O. Wilson. 1967. The theory of island biogeography. Mongr. Popul. Biol. No. 1. Princeton Univ. Press, Princeton, NJ.

Marascuilo, L. A. and M. McSweeney. 1977. Non-parametric and distribution free methods for the social sciences. Brooks-Cole, Monterey, CA.

Mathews, W. H., J. G. Fyles, and H. W. Nasmith. 1970. Postglacial coastal movements in southwestern British Columbia and adjacent Washington State. Can. J. Earth Science 7: 690-702.

Mayr, E. 1954. Change of genetic environment and evolution. In Huxley, J., A. C. Hardy, and E. B. Ford (eds.), Evolution as a process. Allen & Unwin, London. pp. 157-180.

Mazurkiewicz, M. 1972. Density and weight structure of populations of the bank vole on open and enclosed areas. Acta Theriol. 17: 455-465.

Mazurkiewicz, M. and E. Rajska. 1975. Dispersion of young bank voles from their place of birth. Acta Theriol. 20: 71-81.

McCabe, T. T. and I. M. Cowan. 1945. *Peromyscus maniculatus macrorhinus* and the problem of insularity. Trans. R. Canadian Inst. 1: 172-215.

Millar, J. S. 1977. Adaptive features of mammalian reproduction. Evolution 31: 370-386.

Mobedi, I. and F. Arfaa. 1971. Probable role of ground beetles in the transmission of *Capillaria hepatica*. J. Parasit. 57: 1144-1145.

Momma, K. 1930. Notes on modes of rat infestation with *Hepaticola hepatica*. Ann. Trop. Med. and Parasit. 24: 109-113.

Myers, J. H. and C. J. Krebs. 1971. Sex ratios in open and enclosed vole populations: demographic implications. Am. Nat. 105: 325-344.

Nelson, L., Jr. and F. W. Clark. 1973. Correction for sprung traps in catch/effort calculations of trapping results. J. Mammal. 54: 295-298.

Nichols, J., W. Conley, B. Batt, and A. Tipton. 1976. Temporally dynamic reproductive strategies and the concept of r- and K-selection. Am. Nat. 110: 995-1005.

Petticrew, B. G. and R. M. F. S. Sadleir. 1970. The use of index trap lines to estimate population numbers of deermice (*Peromyscus maniculatus*) in a forest environment. Can. J. Zool. 48: 385-389.

________________. 1974. The ecology of the deer mouse *Peromyscus maniculatus* in a coastal coniferous forest. I. Population Dynamics. Can. J. Zool. 52: 107-118.

Redfield, J. A. 1976. Distribution, abundance, size and genetic variation of *Peromyscus maniculatus* on the Gulf Islands of British Columbia. Can. J. Zool. 54: 463-474.

Roff, D. A. 1974. The analysis of a population model demonstrating the importance of dispersal in a heterogeneous environment. Oecologia (Berlin) 15: 259-275.

Rose, R. K. and W. D. Heuston. 1978. Wound healing in meadow voles. J. Mammal. 59: 186-188.

Rowe, J. S. 1972. Forest Regions of Canada. Dept. of Fisheries and the Environment. Canadian Forest Service Publication No. 1300. Ottawa.

Sadleir, R. M. F. S. 1965. The relationship between agonistic behavior and population changes in the deer mouse *Peromyscus maniculatus* (Wagner). J. Anim. Ecology 34: 331-352.

______________. 1970. Population dynamics and breeding of the deer mouse (*Peromyscus maniculatus*) on Burnaby Mountain, British Columbia. Syesis 3: 67-74.

______________. 1974. The ecology of the deer mouse *Peromyscus maniculatus* in a coastal coniferous forest. II. Reproduction. Can. J. Zool. 52: 119-131.

Sadleir, R. M. F. S., K. D. Casperson, and J. Harling. 1973. Intake and requirements of energy and protein for the breeding of wild deer mice, *Peromyscus maniculatus*. J. Reprod. Fertil. Suppl. 19: 237-252.

Schaffer, W. M. 1974. Optimal reproductive effort in fluctuating environments. Am. Nat. 108: 783-790.

Sheppe, W. 1965. Island populations and gene flow in the deer mouse *Peromyscus leucopus*. Evolution 19: 480-495.

Simberloff, D. S. 1974. Equilibrium theory of island biogeography and ecology. Ann. Rev. Ecol. and Syst. 5: 161-182.

Sokal, R. R. and F. J. Rohlf. 1969. Biometry. W. H. Freeman, San Francisco, CA.

Soulé, M. 1966. Trends in the insular radiation of a lizard. Am. Nat. 100: 47-64.

Southwick, C. H. 1955. Regulatory mechanisms of house mouse populations: social behavior affecting litter survival. Ecology 36: 627-634.

Southwood, T. R. E., R. M. May, M. P. Hassell, and G. R. Conway. 1974. Ecological strategies and population parameters. Am. Nat. 108: 791-804.

Stearns, S. C. 1976. Life history tactics: A review of the ideas. Q. Rev. Biol. 51: 3-47.

Sullivan, T. P. 1977. Demography and dispersal in island and mainland populations of the deer mouse, *Peromyscus maniculatus*. Ecology 58: 964-978.

Tamarin, R. H. 1977a. Reproduction in the island beach vole, *Microtus breweri* and the mainland meadow vole, *Microtus pennsylvanicus*, in southeastern Massachusetts. J. Mamml. 58: 536-548.

________________. 1977b. Demography of the island beach vole (*Microtus breweri*) and the mainland meadow vole (*M. pennsylvanicus*) in southeastern Massachusetts. Ecology 58: 1310-1321.

________________. 1977c. Dispersal, population regulation, and K-selection in field mice. Am. Nat. 112: 545-555.

________________. 1977d. Dispersal in island and mainland voles. Ecology 58: 1044-1054.

Terman, C. K. 1968. Population dynamics. In King, J. A. (ed.), Biology of *Peromyscus*. Spec. Publ. No. 2 Am. Soc. Mammal. pp. 412-450.

Terman, C. K. and J. F. Sassaman. 1967. Sex ratio in deer mouse populations. J. Mammal. 48: 589-597.

Thiele, H-U. 1977. Carabid beetles and their environments. Zoophysiology and Ecology 10, Springer-Verlag, New York.

Ullyett, G. C. 1950. Competition for food and allied phenomena in sheep blowfly populations. Phil. Trans. R. Soc. Lond. 234: 77-174.

Van Valen, L. 1971. Group selection and the evolution of dispersal. Evolution 25: 591-598.

________________. 1973. Pattern and the balance of nature. Evolutionary Theory 1: 31-49.

Wallace, A. R. 1869. The Malay Archipelago. MacMillan and Co., London.

________________. 1880. Island Life. MacMillan and Co., London.

Webb, W. L. 1965. Small mammal populations on islands. Ecology 46: 479-488.

Wilbur, H. M., D. W. Tinkle, and J. P. Collins. 1974. Environmental certainty, trophic level and resource availability in life history evolution. Am. Nat. 108: 805-817.